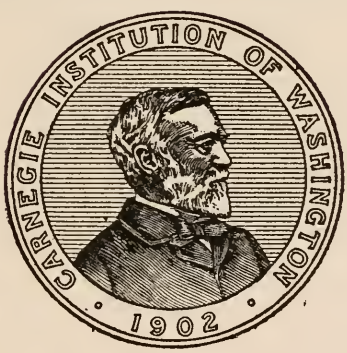
AERATION AND AIR-CONTENT

THE RÔLE OF OXYGEN IN ROOT ACTIVITY

BY

FREDERIC E. CLEMENTS



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AERATION AND AIR-CONTENT.

INTRODUCTION.

Recent studies of the so-called bog xerophytes have shown the air-content of the soil to be an ecological factor of primary and often of unique importance (Clements, 1916, 1920; Dosdall, 1919; Bergmann, 1920). In organizing a comprehensive investigation of bog and swamp plants and of related problems, it has become desirable to analyze much of the literature dealing with the respiration of roots and with anaerobiosis. An attempt has been made to present a complete digest of the results in so far as they have to do with transpiration, growth, or movement, or serve to throw light upon the mooted questions of bog toxins, acid soils, or toxic exudates. In addition, a complete account is given of the development of views upon bog xerophytes and soil toxins, primarily to afford a clear grasp of existing opinion and to reveal the points to which further study should be directed.

In spite of the enormous amount of work done upon the respiration of roots and the significance of soil-air, physiologists and ecologists generally have ignored this subject or have given it little consideration. A cursory survey of a score of text-books shows that the air-content of the soil is not even mentioned by the majority, while it is given slight attention by a few, and accorded recognition as a factor of primary importance by three or four only. This was probably a natural outcome of the laboratory development of physiology. At least, it appears certain that the basic importance of the air-content of the soil could not be appreciated fully until ecology had begun the instrumental measurement of the habitat. Even the latter has found it difficult to distinguish between sequelæ and causes in this field (Plant Succession, p. 90), and general recognition of air-content as a primary factor in many habitats, and a controlling one in wet soils and water, is yet to come.

In the following treatise, the development of our knowledge of the respiration of roots and other underground parts is first taken up in historical sequence, together with an account of studies dealing with the nature and composition of soil-air. This is succeeded by a digest of results in the field of anaerobic respiration, with especial reference to its relation to germination, growth, and movement. A section is devoted to bog xerophytes and swamp plants, with which are considered bog toxins and acid soils, while soil toxins and toxic exudates are discussed in a final section.

I. RESPIRATION AND OXYGEN.

NORMAL RESPIRATION OF ROOTS.

The necessity of oxygen for the proper functioning of roots has not only been repeatedly demonstrated by direct experiment, but further evidence of it has also been gained from the behavior of other organs. This would be expected from the fact that the basic responses of protoplasm are more or less identical for all green plants. As a consequence, studies of the oxygen requirements of leaves and shoots have likewise much significance for the behavior of roots. In the case of underground shoots, rootstocks, tubers, bulbs, and corms, the process of respiration is not only identical with that of roots, but the relation to the air-content is also the same. This is true to a large extent of all soil organisms and especially of the host of aerobic fungi. Soil algæ, on the contrary, free more oxygen than they use and serve to maintain the air-balance of the soil.

In organizing the evidence derived from the results of many investigators, it has been desirable to preserve the historical sequence as far as possible, but at the same time to give a coherent discussion of the various phases of the subject. In consequence, our knowledge of the oxygen requirements of roots is divided into three sections, namely, normal respiration, anaerobic respiration, and field studies of aeration. Each of these furnishes its own particular body of evidence and all must be taken into account for a complete view. For convenience, the first two have been divided into three general periods determined by the years 1870 and 1900. One of these marks the first studies of intramolecular respiration by Pfeffer and his students, and the other the beginning of quantitative ecology, as well as a more intensive attack upon the problems of respiration by Palladin, Stoklasa, Nabokich, and their associates.

Early researches.—The importance of oxygen for germination and growth was first demonstrated toward the close of the seventeenth century by several investigators. The first of these were Mayow (1668), who found that oxygen was indispensable to plants, and Huygens and Papin (1674), who showed that plants die under the air-pump in the absence of air. Malpighi (1687) was the first to determine that air was required for germination, while Ray (1690) discovered that lettuce seeds would not germinate in a vacuum, but did so readily upon the return of air. Homberg (1699) found that the seeds of *Portulaca oleracea*, *Lactuca sativa*, and *Lepidium sativum* germinated slowly or not at all in rarefied air.

Hales (1727) first discovered that CO_2 was secreted by roots. Corti (1774 : 210) placed plants of *Chara* in a vacuum and left them

for 48 hours. The movement of the protoplasm ceased, but it began again in 8 to 12 hours after the plants were returned to atmospheric air. Scheele (1777) was the first to prove that oxygen was used during germination and carbon dioxid released, as in animals. Ingenhousz (1779) was the pioneer in recognizing that plants give off carbon dioxid at night or in the dark, in contrast to the evolution of oxygen during the day. He stated that roots, flowers, and fruits, as well as green parts, behaved in this manner. In 1796, he emphasized the fact that roots and other colorless parts always excrete CO_2, while green parts in the light give off oxygen. He likewise denied that plants absorb their necessary carbon from the soil by means of the roots.

Senebier (1791) stated that the access of air is indispensable to plant life and that it was likewise necessary to the germination of seeds in the soil. He also pointed out that the roots of plants perish in stagnant water. Huber and Senebier (1801) found that the amount of air during germination diminished in proportion to the oxygen in it, and that this was accompanied by the formation of carbon dioxid. They likewise noted that seeds would not germinate in air whose oxygen had been exhausted by bees and they confirmed the need of oxygen for plant-growth by a comprehensive series of studies in various gases. Rollo (1798) believed that oxygen disappeared and was replaced by carbon dioxid in the course of germination, and he determined that barley grains gave off CO_2 for several days in the absence of oxygen.

Saussure (1804) regarded water and oxygen as the two factors essential to germination and stated that a small amount of oxygen is present even in the case of the seeds of water-plants and others that germinate under water. He proved this by showing that peas, lentils, and seeds of *Alisma* and *Polygonum* were unable to germinate in an amount of boiled water 7 to 8 times their weight, but did so readily when the amount was 200 times greater. He further showed that oxygen disappears and is replaced by carbon dioxid when the seeds are in direct contact with it, but, when oxygen is scanty or lacking, decomposition results, with the evolution of hydrogen as well as carbon dioxid. The amount of oxygen necessary to effect germination differed with the species, beans, kidney-beans, and lettuce requiring more than peas, and these more than wheat, barley, or purslane.

Roots of carrot consumed their own volume of oxygen, as did turnip, while a potato used 0.4 of its volume and a lily-bulb approximately the same. These differences were reflected in those of the leaves. Leaves of deciduous trees and shrubs consumed from 2.2 to 8 times their volume of oxygen in 24 hours, beech and apricot being the most active and lilac the least. The average consumption for the 15 species was approximately 6 times the volume. For

evergreens, both broad-leaved and needle-leaved, the range was from 0.8 to 4 times and the average 2 times the volume. For terrestrial herbs, the range was from 0.5 for *Lilium* to 5 for *Triticum*, and the average 2.4 times the volume. Aquatic and marsh herbs varied from 0.7 for *Alisma plantago* to 2.3 for *Lythrum* and *Carex*, the average being 1.6 times the volume, while the range in fleshy plants was from 0.6 for *Saxifraga cotyledon* to 1.7 for *Sedum* and *Mesembryanthemum*. The average was 1.1 times the volume. In most cases the respiration was 50 to 100 per cent greater in May or June than in September.

To obtain further proof of the need for oxygen, Saussure treated the roots of the chestnut with nitrogen, hydrogen, and carbonic acid, using other plants in atmospheric air as checks. The plants whose roots were in contact with CO_2 died first at the end of 7 or 8 days, while those with the roots in nitrogen and hydrogen died at the end of 13 or 14 days. The chestnuts with roots growing in ordinary air were still vigorous at the end of 3 weeks, when the experiment was finished. The conclusion that the presence of oxygen is necessary for growth was further supported by the observation that plants with roots submerged in stagnant water suffered more quickly than those in running water, and also by the fact that roots which grew into manure or into water conduits became very greatly divided in the endeavor to increase their contact with the very small amount of oxygen found in such places.

Grischow (1819 : 143) determined that roots take up oxygen and give off carbon dioxid. He likewise proved that fungi absorb oxygen and evolve carbon dioxid, and hence that their respiration is essentially the same as that of green plants.

Marcet (1829) thought to have demonstrated that fungi also evolve hydrogen in respiration, but later (1834) concluded that this was due to fermentation processes set up by bacteria and that fungi respired in the usual manner.

Meyen (1838) declared that respiration is general for all plant parts, and he also distinguished clearly between respiration and photosynthesis in the economy of the plant.

Dutrochet (1840) stated that, since all plant parts absorb oxygen and excrete carbon dioxid, they should also produce heat, and he was able to demonstrate this experimentally. He also emphasized the need of distinguishing between respiration and the decomposition of CO_2 in the light, and determined that neither periodic nor tropistic movement was possible in the absence of oxygen.

Becquerel (1833), Wiegmann and Polstorff (1842), and Oudemans and Rauwenhoff (1858) early demonstrated that the excretion of the root was acid, as shown by its reaction to litmus.

Garreau (1851), in the study of respiration in the different organs of various plants, determined the amount of CO_2 exhaled by the

fleshy roots of carrot and the fibrous roots of *Senecio* during 24 hours. The respiration of the latter was more than 6 times greater than that of the former. The amount of CO_2 expired by plants was found to be the greater the richer they were in protein and the more extended surface they presented relative to their mass. When green parts of plants were submerged they respired as aerial plants, but with the difference that the amount of CO_2 was reduced because the medium was poorer in oxygen.

While Liebig (1858) was apparently the first to note the etching of limestone and ascribe it to the action of roots, Sachs (1860, 1865) first demonstrated experimentally that this was the case. He grew the roots of corn on polished marble plates and found that they etched the surface. He concluded that this was due to the excretion of CO_2 from the roots, since roots grown in distilled water quickly charged this with CO_2. He also thought it possible that the corrosion might be due to the acid cell-sap which saturated the cell-wall. His early work was confirmed by experiments in 1860 and 1864, showing the corrosion of the surface of dolomite, magnesite, etc. He assumed that this might be produced by CO_2, but also thought that it might perhaps be due to the acid sap of the roots themselves. He detailed at some length the studies of 1864 with several species of plants on various surfaces. According to Mayen (1838, 1:11), Moldenhawer thought that the root-hairs secreted a sap which served to dissolve any other material.

Knop (1861, 1864) confirmed the results of Sachs in regard to root excretion. He found that a considerable amount of CO_2 accumulated during the growth of grasses in neutral solutions. In further researches, proof was obtained that CO_2 was excreted by the roots of growing plants and this was regarded as a device for increasing the absorption of solutes. He concluded that all organs absorb oxygen in producing CO_2, and hence that the tissues of land plants were filled throughout with air containing CO_2. It was regarded as probable that the CO_2 excreted by the root serves universally for the solution of mineral substances in the soil, and as possible also that other more permanent acids aid in this work.

Nobbe (1865) showed that potato tubers respire during storage in the winter and that the amount of starch was correspondingly reduced. Fleury (1865) confirmed the results of Huber and Senebier and of Saussure in showing that dry seeds begin to evolve carbon dioxid soon after the absorption of water.

Corenwinder (1867 : 63) grew roots of *Cuphea* attached to the aerial parts in air with a known quantity of CO_2 in order to determine whether roots absorb the latter. He found, on the contrary, that a considerable amount of CO_2 was exhaled in the case of a number of roots. Similar experiments were made with cabbage and with *Eupatorium* with the same results. The author found, more-

over, that certain marsh plants died quickly when their roots were kept in contact with water charged with CO_2.

Later researches.—As a consequence of the work of Pfeffer and his students, active investigation was directed more to the problems of intramolecular respiration, and direct results relating to normal respiration were largely a by-product. Extensive studies were made, however, of the respiratory curve and quotient during germination and growth at the beginning of this period by Wiesner (1871), Sachsse (1872), Heintz (1873), Dehérain and Landrin (1874), Dehérain and Moissan (1874), Wolkoff and Meyer (1874), Meyer (1875), Borodin (1875), Detmer (1875), Rischawi (1876), and Saikewicz (1877). Sachsse and Detmer in particular, together with Müntz (1876), Dehérain and Vesque (1876, 1877), and Bonnier and Mangin (1884), gave complete confirmation to the earlier results, which had showed that carbon dioxid was the only gas produced by respiration in all green plants and in most fungi. At the end of this period Pfeffer (1878) declared that it was impossible to ascribe any of the energy used by higher plants to intramolecular respiration, and that the share of oxygen in metabolism was so important that normal functioning was impossible in its absence. He regarded the old maxim, "No life without respiration," as still effective, since normal respiration is indispensable if the organism is to remain capable of life.

In his study of the respiration of water plants (1875 : 694), Böhm reached the conclusion that the amount of oxygen used in the respiration of water plants in atmospheric air is much smaller than under similar conditions in the case of land plants. Likewise, carbon dioxid is formed by water plants in an atmosphere completely without oxygen or otherwise indifferent, in consequence of intramolecular respiration, but more feebly than under similar conditions with land plants. Freyberg and Mayer (1879 : 463) studied the respiration of swamp plants with special reference to the comparative behavior of swamp plants and land plants. They proceeded upon the assumption that the presence of air-passages was supplemented by a difference in the intensity of respiration in the roots of swamp plants. Their chief results are expressed in table 1.

The respiration maximum for the roots of mature swamp plants was 38 c.c. O, and for seedling roots it was 56 c.c. O, while the corresponding maxima for mesophytes were 68 and 83 c.c. The respiration was found to increase with the nitrogen-content, and this was thought to explain why swamp and water plants have a uniformly low respiration. The final conclusion was that the roots of swamp plants require less oxygen than those of mesophytes, whether this be determined with respect to volume, mass, or dry weight.

TABLE 1.—*Respiration of roots and leaves.*

Species.	Root-length (equal volume).	Oxygen used in 24 hours per 1 gm. dry weight.	Per cent of nitrogen in dry weight.
Roots.			
Seedling	*mm.*	*c.c.*	
Triticum vulgare	15.6	67.9	3.2
Do	35.0	82.8	.....
Oryza sativa	14.6	44.4	1.6
Do	27.6	55.1	.....
Mature.			
Lamium album	29.0	62.5	3.4
Mentha aquatica	13.2	37.2	1.5
Ranunculus bulbosus	39.0	46.1	2.7
Caltha palustris	41.0	19.1	1.7
Do	37.0	27.5	.....
Leaves.			
Phleum pratense	.....	27.2	4.2
Do	.....	29.4	.....
Lolium italicum	.....	22.4	3.0
Do	.....	24.7	.....
Do	.....	24.8	.....
Phragmites communis	.....	15.0	2.6
Do	.....	12.8	.....
Glyceria fluitans	.....	11.8	1.9
Do	.....	11.2	.....
Ranunculus bulbosus	.....	29.6	4.6
Ranunculus fluitans	.....	18.9	2.9
Do	.....	19.2	.....

Cauvet (1880 : 113) demonstrated that roots constantly excrete CO_2 and that this excretion is weaker at night than during the day. He also determined that the root does not absorb CO_2 from the soil, and that the CO_2 excreted has for its immediate effect the solution of the solid matter of the soil for the use of the root.

Schwarz (1883 : 135) at first assumed that the production of root-hairs was suppressed in many plants because of lack of oxygen. The addition of abundant oxygen to the water-cultures failed to cause the production of hairs and he concluded that the absence of hairs could not be ascribed to its lack. It seems probable, however, that the amount of oxygen used was too great for growth. Van Tieghem and Bonnier (1882) found that 7.976 gm. of peas, sealed in air, yielded 3.82 per cent of carbon dioxid and reduced the oxygen to 14.44 per cent in the course of 2 years.

Bonnier and Mangin (1884 : 215, 220) pointed out that, in prolonging the sojourn of plants in containers, the respiration was no longer normal. At the end of a certain time, when nearly all the oxygen was consumed, fermentation proper entered and carbon dioxide was released in great quantity without oxygen being absorbed. They were also (1885) the first to show that respiration increases with increased humidity of the air.

Müller-Thurgau (1885 : 857) found that potato tubers respired more vigorously just after being harvested than they did several days later. But tubers that were separated from sound stocks respired about doubly. Ultimately, however, the respiration sank to about the same level and then remained constant for a long time during the resting condition of the potato.

In an investigation of the relation of cell-turgor in growing organisms to respiration, Palladin (1886 : 328) reached the following conclusions: Since the absorption of oxygen is necessary for the production of substances which cause turgor, it is to be expected that the latter will be reduced by lack of oxygen, and, in fact, plants that have lived some time without oxygen appeared to be withered. In growing organs the accumulation of the organic acids that produce the turgor of the cells appears as a result of respiration. In the absence of oxygen, growth ceases on account of the interruption of the formation of these substances.

Molisch (1887 : 84) studied the secretions of roots and concluded that they influence also organic materials, and in a higher degree than mineral and rock constituents of the soil. He found that the root-secretions have both reducing and oxidizing action. They oxidize different organic substances, such as guaiaconic, pyrogallic, and gallic acids, and, most important of all, humus substances. As a consequence, they favor in a high degree the decomposition of the organic material of the soil of fields and of forests. The root-secretion changes cane sugar to reducing sugar, and exerts a weak diastatic effect.

Kny (1889 : 163) found that a 12-day exclusion of oxygen prevented the formation of cell-walls, but was not sufficient to kill the cells completely. He concluded that the free oxygen of the air is not only necessary for the beginning of the formation of cell-divisions in the wound-periderm, but also for cutinization of the membrane. The cell-divisions of the latter seem to be favored a little by the action of a very small amount of hydrogen peroxide.

Loven (1891) studied the respiration of a number of marine algæ, *Ascophyllum, Laminaria, Ulva, Enteromorpha, Ceramium,* etc., and found that they are able to absorb every trace of oxygen present in the water. In water entirely free from oxygen, algæ can produce considerable quantities of CO_2. He gave the oxygen-content per liter and also that of CO_2 before and after the respiration experiments.

Aubert (1892 : 280) showed that the internal air of fleshy plants differed considerably from the atmospheric air in the relative proportions of the component gases. The variations in the $\frac{CO_2}{O}$ ratio in the fleshy plants bore a certain relation to the amount of water they contained. They were greater when succulence was most pronounced. Fleshy plants subjected to the same temperature in the dark absorbed a nearly constant volume of oxygen, but evolved

during the day a greater amount of CO_2 than at night. This difference between the day and night volumes of CO_2 was more important when the plants were most fleshy. Plants exhibited a more active gas-exchange in proportion as their fleshiness is less pronounced, and hence ordinary plants showed a greater respiration intensity than fleshy ones. Among fleshy plants, *Crassulaceæ* and *Mesembryanthemaceæ*, which possess a thin cuticle, exhibited a more active exchange than most of the *Cactaceæ*. The fleshy euphorbias and trees with evergreen leaves were nearly intermediate in this respect. The extent of surface-contact with the atmospheric air was regarded as of the first importance in explaining differences in intensity and respiration, and the amount of water the plant contains as next most important.

Aeroboe (1893) studied the respiration of roots of *Vicia faba* in relation to light and reached the conclusion that this exerted an indirect effect. He found that when plant parts were placed in the dark the production of CO_2 steadily decreased.

Böhm (1893), in a study of the respiration of potatoes, found that wounding, relatively low and high temperatures, partial exclusion of oxygen, continued exposure to pure oxygen, and infection by *Phytophthora infestans*, all produced energetic respiration. In a medium poor in oxygen, thin cylinders of sound or stimulated tubers used only a small amount of the gas.

Mangin (1896 : 747) in experiments with flax, radish, peas, carrots, etc., found that the accumulation of CO_2 and a reduction in oxygen effects a diminution of respiratory activity in the seeds and tubers. This occurred in air that contained 1 to 3 per cent of CO_2 in one case and 2 to 5 per cent in the other.

Jost (1893 : 100) observed that wounded potatoes, especially those cut into many pieces, showed earlier growth of the buds. Ziegenbein (1893 : 594) determined the respiration rate of potato tubers, seedlings, and shoots at different temperatures to be as follows, expressed in milligrams of CO_2 produced by 100 gm. in an hour.

Czapek (1896 : 321) studied the excretions of roots of *Phaseolus*, *Pisum*, *Helianthus*, *Cucurbita*, *Zea*, *Linum*, *Picea*, etc., in water and in air saturated with moisture. He found that the roots of all of these secrete various substances, partly organic, partly inorganic. The latter are potassium, calcium, magnesium, and hydrochloric, sulphuric, and phosphoric acids. Of these, only potassium and phosphoric acid are present in any considerable

TABLE 2.

Temp.	Potato tubers.	Seedlings, *Vicia faba*.	Shoots, *Abies excelsa*.
° *C.*			
10	1.17	.....	.....
20	2.22	.....	.....
30	4.62	55.20	185.00
35	7.85	78.72	206.40
40	10.24	65.10	198.40
45	12.22	57.80	168.90
50	11.14	80.80	33.30
55	10.30	.....	.....
60	2.71	.....	.....

quantities, and they occur in the form of primary potassium phosphate. Acetic acid and lactic acid are not found in the root excretions, but formic acid in the form of potassium salts is not at all rare. This diffuses out of the living cells of the root-tips, and is, therefore, not a product of decomposition. Oxalic acid, as calcium oxalate, was found but once, in the excretions of *Hyacinthus orientalis*. The corrosion phenomena produced by roots are due in the largest degree to the excretion of CO_2. The reddening of litmus paper and the corrosion of rock surfaces is due to two different substances, carbon dioxid and monopotassium phosphate. No acid other than CO_2 is regularly excreted by the roots of higher plants. The excretion of diastatic or inverting ferments by the roots of higher plants is not physiologically impossible, but a critical repetition of the experiments of Molisch, who assumed the regular occurrence of these ferments in the root-secretions, gave only negative results.

Richards (1896 : 551) determined that a greatly increased respiration results after injury to plant-tissue, varying in intensity and duration with the character of the tissue and the extent of the wound. This increased activity usually reaches a maximum within two days and then falls gradually to the normal as the wound heals over.

Palladin (1897:827) concluded, since completely immersed etiolated leaves do not become green, that oxygen, to an amount greater than that freed in assimilation, is necessary for the production of chlorophyll.

Wacker (1898 : 70) has studied the effect of soil and water upon water and land plants. He found that *Vicia faba*, *Lupinus albus*, *Helianthus annuus*, and *Cucurbita pepo* undergo a retardation in the growth in length of their main roots when they are cultivated in water. On the other hand, such water plants as *Lemna minor* and *trisulca*, *Azolla filiculoides*, and *Hydrocharis morsus-ranæ*, in a normally moist garden soil, show almost no root-growth. In both cases this difference in growth is not a consequence of the different amount of oxygen in the two media, or of the greater density of the soil solution. The almost complete cessation of root-growth in *Lemna minor* in soil seems to indicate that these plants do not have the ability to draw water from the soil particles in sufficient amount. Roots are only formed when the soil is saturated with water, so that the plant may come in intimate contact with the water in the soil. In mud, the roots of land plants, *Vicia faba* and *Lupinus albus*, died off, either due to the absence of free oxygen, to the presence of various decomposition products, or to both of these factors together. While swamp plants are able to secure a sufficient amount of oxygen for the roots from the aerial parts, land plants are unable to do this, owing to the absence of aeration passages.

Recent researches.—Mazé (1900 : 350) found that a short immersion of seeds in water restricted their further germination and that

after 8 to 12 days they completely lost their power of growth and died for the most part.

Arker (1901 : 431) investigated the influence of the surrounding medium upon roots and showed that the rate of growth in roots of *Lupinus albus* was increased when a stream of atmospheric air was drawn through the soil and when the soil-air was diluted to a certain degree. The growth of roots of *Lupinus* and *Helianthus* in water was faster when atmospheric air was bubbled through the solution. The growth in mud was promoted by frequently renewing the water and thus increasing the access of air. The retardation of root-growth in water was less marked, since the oxygen is absorbed more readily from water. The drawing of air through water does not increase the oxygen-content, but keeps it nearer saturation.

Strohmer (1903 : 933), in a comprehensive study of the respiration of the sugar-beet, showed that some roots under normal conditions excrete no other carbon-containing gas than CO_2. When wounded, the sugar-beet showed an evident increase in the respiration intensity. Ethyl alcohol was found to be a product of intramolecular respiration.

Newcombe (1902) observed that roots were distorted when grown in closed tubes with water at 23° C. or above, and ascribed this response to the possible absence of oxygen or the accumulation of root secretions.

Vöchting (1902 : 87) studied the influence of aeration upon the germination of potato tubers, chiefly by means of cylinders so arranged that the upper half would have well-aerated soil and the lower half soil in which oxygen was more or less absent. In other experiments, three layers of different air-content were arranged in each cylinder. In the case of cylinders of two layers, the upper produced many shoots and none or relatively few tubers, while in the lower the results were just opposite. In the cylinders with more than two layers, the access of oxygen to the lowermost was so reduced that these decayed before further results could be obtained. In the two upper layers the results were as indicated above. In testing Stich's discovery that 3 to 4 per cent of oxygen did not measurably decrease the amount of CO_2 produced, tubers were placed in an atmosphere of 4 per cent. After a few days sprouts appeared and the amount of oxygen was then reduced to 3 per cent. Under these conditions new sprouts still appeared and the oxygen was then reduced to 2 per cent, where no further growth occurred. The shoots apparently remained fresh and the experiment was continued for 4 weeks, when it was found that all tubers had decayed more or less. He also found that the roots of potato tubers ceased to produce root-hairs when the amount of oxygen was reduced to 3 per cent. In experimenting with willow twigs, he showed that there was enough oxygen in the water to maintain life, but not for the production

of new organs, and that an aerial supply was needed for the growth of shoots and roots.

Smirnoff (1903 : 26) has shown that wounding causes an increase in the intensity of normal respiration in the bulbs of *Allium*, but not of intramolecular respiration. This increase may sometimes amount to more than 50 per cent.

Kossowitch (1904), in studies with hemp, has reached the conclusion that the respiration of roots is significant, and that it can not be left out of consideration in the biological processes of the soil.

Pütter (1904) found that *Beggiatoa* and *Euglena*, as well as *Paramœcium* and *Spirostomum*, were obligate aerobes that were harmed by very low oxygen pressures, while complete withdrawal of oxygen killed them with great rapidity.

Duval (1904 : 76) has shown by studies of the seeds of beans, cabbage, carrot, lettuce, and onion that the respiration of seeds is intense if moisture be present and is accompanied by a rapid loss in vitality. Table 3 gives the results when seeds were allowed to absorb from 4 to 10 per cent of water.

TABLE 3.

Kind.	Weight.	CO_2 per year.	Germination.	
			Exper.	Control.
	grams.	*c.c.*		
Beans	25	2.5	86	100
Cabbage	10	24.0	0	89
Carrot	10	27.0	0	84
Lettuce	10	19.5	0	94
Onion	10	26.5	0	97

When onion seeds were kept for a year and 13 days in sealed bottles of air or illuminating gas, the vitality was not impaired except in the case of those with additional moisture, which were all dead. In this bottle the oxygen had completely disappeared and the amount of CO_2 was 13.35 per cent, while in the two other bottles containing air, the oxygen was 8 and 12 per cent and the carbon dioxid was 18.8 and 6.8 per cent.

Snow (1905 : 33) found that the absence of oxygen stopped the production of root-hairs and retarded growth, while root-hairs also developed better in tap-water than in distilled water. In the case of corn, the reduction of the oxygen-pressure to zero completely suppressed the development of hairs, even when the CO_2 was removed. The roots of wheat quickly died in the absence of oxygen, but in the case of several roots that lived for a day, no root-hairs were formed. The roots of willow twigs developed root-hairs in about half the normal oxygen-content, but this may have been due

to the presence of chlorophyll or to included air. Bergmann (1920 : 17) and Cannon and Free (1920 : 62) have likewise shown that the formation of root-hairs is dependent upon oxygen. Raciborski (1905 : 338) found that the ability of the root-surface to oxidize easily oxidized substances about it is controlled by oxygen.

Stoklasa and Ernest (1905 : 723) pointed out that roots act strongly upon rock through the excretion of CO_2, as is often seen in nature on smooth stone-walls corroded by roots. This effect has often been ascribed to organic acids produced in the roots, but it is now clear that this rôle is played only by the CO_2, and it is particularly noticeable in young root-systems. This makes it possible to understand how the plant prepares its necessary mineral nutrients in solution through its root-system. This results from the excretion of CO_2 by its own root-system and through the micro-organisms of the soil, the number of which is materially increased in cultivated soils.

Brizi (1906 : 89) found that the roots of rice are not of the aquatic type, and demonstrated by means of water-cultures that oxygen is absolutely essential for their growth. He concluded that the algæ of the rice-fields are doubly useful, in that they utilize a large amount of CO_2 and set free a corresponding quantity of oxygen available for the roots.

Day (1906 : 37) has grown wheat, barley, oats, and peas in jars, one set of which was aerated daily during the growing season by drawing enough air through to completely change the air in the jars. In germination there was no marked difference between the two sets, except in the case of the peas. The aerated jars germinated 81 per cent and the unaerated ones 61 per cent. Moreover, the growth of the pea plants was nearly twice as great in the aerated as in the unaerated jars for the first period. There was but little difference between the grains grown in the aerated and unaerated conditions. In a second study of aeration (1907 : 36), alfalfa and soy beans were grown in addition to wheat, barley, oats, and peas. There were four jars of each species and air was forced through two of them once a day. The results for wheat and barley were negative, while oats and peas yielded slightly better when aerated. This lack of response was thought to be due to the fact that frequent rain produced good natural aeration in all jars. One striking fact was that the pea plants grown from seed from the aerated jar of the previous year gave double the yield given by the plants from seed from unaerated jars. Alfalfa and soy beans did not mature, but the beneficial effect of increased aeration was very noticeable.

Hall (1906 : 57) concluded that from several points of view it is not necessary to assume the existence of an excretion from the roots of a plant of a permanent acid, organic or inorganic, to attack the solid mineral particles of the soil and to bring them into solution for the nutrition of the plant. The growing portions of a plant-root are

always giving off CO_2, and CO_2, especially in the concentrated solution which must be momentarily formed in the cell-wall of the root-hairs, has an appreciable solvent effect upon the majority of the minerals composing the soil. This CO_2 alone is capable of giving rise to such solutions as are required for the nutrition of the plant. As the direct evidence is also adverse to the idea of an excretion of acid, the principle of not seeking remote causes would lead us to attribute to CO_2 only, the long-recognized solvent power of the plant upon the soil.

Kunze (1906) has shown that corrosion studies and culture experiments in powdered stone prove that the higher plants can not obtain necessary nutrients from unweathered stone. Moreover, plants which are marked by vigorous excretion of acid, such as white cabbage and vetch, show a stronger development, due to the energetic decomposition of the soil than those with more or less of this quality, e. g., mustard and sainfoin. Rapidly growing plants of relatively short vegetation period show marked excretion, e. g., *Cucurbita*, *Helianthus*, *Phaseolus*, *Zea*, etc. Among the grasses, *Secale* and *Avena* show strong excretion, *Hordeum* and *Triticum* less. Moreover, while the ability of the grasses to dissolve soil nutrients through root excretions is small or lacking, this is compensated by the greatly branched root-systems and their energetic transpiration. The marked excretion found among the *Boraginaceæ* is explained by the vigorous development of the plant-body, relative short vegetative period, and the dry habitat. Since only a small amount of acid or none at all is produced by a great number of plants, and since in many cases CO_2 plays only a subordinate part in breaking down the soil particles, it is assumed that many higher plants must possess another means of producing nutrient solutions in the soil, as by the aid of soil fungi.

Stoklasa and Ernest (1908 : 64), in a study of the chemical nature of the root secretion, conclude that carbon dioxid is the sole gas secreted in normal respiration. The injurious action which the lack of oxygen in the soil produces upon the root is evident, and appears especially in soils crusted over or supersaturated. The unsatisfactory aeration of the soil always produces certain pathologic phenomena of the plant, which can only be connected with the improper oxidation of the products of the decomposition of the carbohydrates and proteins.

Grüss (1907 : 69) studied the chemical changes involved in wounded potatoes and found the oxidizing and diastatic enzymes increased. Wismewski (1912 : 1045) found that the rest-period of buds of *Hydrocharis morsus-ranæ* was shortened by wounding. Müller-Thurgau and Schneider-Orelli (1910 : 309; 1912 : 386) observed increased respiration in potato tubers and bulbs of *Convallaria* after the warm-bath, as did Iraklionow (1912 : 515) in potato

tubers after treatment with warm water. Hoffman and Sokolowski (1910) showed that varieties of potatoes differed among themselves in the intensity of respiration and the evolution of carbon dioxid, and that the effect of water and nitrogen-content was not always the same as in grains, since potatoes with high water and protein content may respire less actively than those with low water and protein.

Appleman (1914) found that potato tubers could be sprouted at any time during the rest period by removing the skin and supplying proper conditions for growth, including the maximum partial oxygen-pressure of the atmosphere. Subdued light stimulates growth in buds on new tubers with slightly suberized skins, probably owing to the greater oxygenation of the tissues by photosynthesis, as this disappears when the skin is removed. The rest-period in new potatoes is shortened by treatment with hydrogen peroxide, which is decomposed by catalase in the tissue, liberating free oxygen. It is concluded that the elimination or abbreviation of the period of rest is correlated with increased absorption of oxygen.

In a study of the relation of catalase and oxidases to respiration in the potato tuber (1916 : 223) Appleman determined the rate of respiration and the activity of catalase and the oxidases under a variety of conditions. He confirmed his earlier result that exposure to ethyl bromide gas greatly increased respiration, and found a similar increase in the catalase activity, but none in that of the oxidases. The effect of cold storage was to nearly treble the respiration, and to increase catalase activity nearly 50 per cent, while slightly reducing oxidase activity. Greening increased respiration and catalase activity a little and reduced slightly the oxidase action. The former were also greater in the seed end than the stem end, while the latter was practically the same. A difference of about 40 per cent in the respiration of two varieties was closely reflected in the catalase, but not in the oxidase activity. The author's conclusion is that there is no correlation between oxidase activity and the rate of respiration, but a very striking one between this and the catalase activity of the potato juice. He also finds (1918 : 209) that the catalase activity of the juice of sweet corn is a fair index of the respiration of the tissues, and concludes that catalase activity is invariably correlated with the oxidation processes of respiration.

Crocker and Harrington (1918 : 171) have shown that there is a similar correlation between catalase activity and respiration in the seeds of Johnson grass, but not in those of *Amarantus*. As a rule, the catalase activity of seeds seems to parallel physiological behavior much more generally than does oxidase activity.

Bartholomew (1913, 1915) applied the name blackheart to a disease of the potato tuber in which much of the tissue is dead and black. He showed that it was due to tissue change caused by overheating

in an atmosphere with insufficient oxygen to meet the demands of rapid respiration. Experiments proved that the only conditions necessary for the production of blackheart were excessive temperatures and insufficient oxygen.

Stewart and Mix (1917 : 277) found that no sprouts start and any already present blacken and die when jars full of potatoes are sealed at 70° F. Moisture appears on the surface of tubers after 10 days and the condition of blackheart develops in the interior. The amount of air for the proper maintenance of tubers was determined by two series of experiments. When the number of volumes of air ranged from 4.6 to 9.5 per volume of potatoes, sprouts barely started and were dead at the end of 40 days. From 10.5 to 14.7 volumes they were very feeble, and were likewise dead at the end. With 15.7 to 18.5 volumes the growth was feeble and the sprouts dead, while at 19.7 to 33.2 volumes the sprouts were normal. In the one series examined for it, blackheart was present from 4.6 to 22.2 volumes.

Coville (1910) has emphasized the importance of good aeration for the swamp blueberry and other heaths. The ideal condition of the peat about the roots is one of constant water-content during the growing-season, but with such drainage that thorough aeration is secured. The high degree of aeration obtained is thought to explain the success attending the use of coarse kalmia peat, since pure peat was not used by the earlier heath-growers. Without understanding the importance of air, they secured aeration by mixing pieces of pots or sandstone with the soil.

Shull (1911 : 476) decided that the seeds of *Xanthium* can not grow without comparatively large amounts of oxygen, while the naked embryos of the two seeds require very different amounts of oxygen for germination. The delay in germination is largely due to the nature of the coats which exclude the oxygen. In a later study (1914 : 64) he was able to show that the seed-coats of seeds of *Xanthium glabratum* used 20 per cent as much oxygen as the seeds themselves. The respiration of the lower seeds was greater than that of the upper in a ratio of 1.35 : 1. The lower seeds with coats off used from 2 to 5 times as much oxygen as those with the coats on.

Babcock (1912 : 111) found that, while intramolecular respiration might occur in seeds containing more than 10 per cent of water, germination never took place except when direct respiration was possible. Free oxygen was essential, though it was not always necessarily present in the gaseous state. Some seeds in water utilize dissolved oxygen, but only those of water plants can grow properly under these conditions. A number of seeds of cultivated plants decomposed hydrogen peroxid rapidly, and then germinated as readily as in the air.

Chambers (1912 : 203) summarizes his results upon the relation of algæ to gases as follows:

"There is an intimate and mutual relation between the algæ and submerged aquatics in a body of water and the gases dissolved in that water. They fluctuate together. Air, or its constituents, oxygen and CO_2, are as essential to water-plants as water is to land-plants, and equally difficult to secure. Warm and stagnant water is poorer in these essentials than colder water gently agitated by wind or currents. Currents are especially beneficial to attached plants by renewing or removing these gases. Some species demand more aeration than others. Some species are more tolerant of stagnant water than others. Filamentous forms with large cells and thin outer walls are best adapted to stagnant waters. Such forms predominate in warm, tropical fresh waters, which are poorly aerated. Stagnant water, on account of the large amount of CO_2 and the small amount of oxygen, favors the formation of colonies and filaments rather than of free individual cells. Colonies and filamentous forms may be produced artificially with some plants by increasing the amount of CO_2 or diminishing the amount of oxygen in the culture solutions. Narrow, much-branched filaments are adapted to and produced by poorly aerated waters. Aeration or abundance of oxygen apparently favors the formation of chlorophyll; and algæ are brighter green when well aerated. The periodicity of spore formation is not readily influenced by aeration or gas content of the water. It seems to be more a matter of heredity."

Hunter (1912 : 183) has grown plants in five different types of soil as follows: (1) soil with small lumps, loose; (2) soil fine, loose; (3) soil fine, firm below with loose surface; (4) soil fine, firm; (5) soil fine, hard. Seeds of *Helianthus*, *Pisum sativum*, *Triticum*, and *Lepidium sativum* were sown in the pots with a more or less equal water-content. The plants made very different growths in the several soils. The roots were longest in pot No. 1 and shortest in No. 5. The plants in the latter were small and the roots were unable to penetrate the soil much below the surface. The plants in the loose fine soil had the largest leaves and the best developed root-system of the series. The differences in growth were attributed to variations in the amount and movement of the soil-air. This was supported by determining the resistance offered to the movement of air through the various soils. The loosest soil was taken as unity and the relative restistance of the other four was as 2, 17, 42, and 310. Further proof was obtained by planting badly developed seedlings with weak stems and curled leaves in soil through which 15 liters of air were drawn each day for 3 weeks. In 2 or 3 days the seedlings subjected to the air-currents became more robust and the stems stronger, while the leaves grew rapidly and became much larger than those of the control plants. By comparative water-cultures, in which one series was not aerated at all, while another had a continuous current of air bubbling through, Hall, Brenchley, and Underwood (1914 : 278) have shown that barley and lupine in the aerated

series gained more than 50 per cent in dry weight over the plants in the non-aerated one.

Harrison and Aiyer (1914 : 93) have determined the beneficial effect of drainage on the growth of rice in pots. The results are shown in table 4.

TABLE 4.

Experiment.	Weight of grain.		Weight of straw and chaff.	
	I.	II.	I.	II.
	grams.	*grams.*	*grams.*	*grams.*
Undrained	11.15	12.15	24.70	21.45
Drained on seventh day	13.47	13.80	19.75	21.80
Drained on third day	14.45	17.65	26.40	27.45
Drained on second day	11.92	14.25	20.57	26.10
Drained every day	12.08	13.60	24.37	26.00

When the drainage was made complete, so that air could enter the soil, there was likewise a definite increase in the production, which reached a maximum between 1 and 2 days' aeration. This was less marked than in simple drainage, however, owing to the greater amount of oxygen in the soil-water as a result of the activity of algæ.

Hole and Singh (1914), in studying the relation of sal (*Shorea robusta*) to air-content, found that germination was best in the well-aerated sandy soil and that it was 8 to 32 per cent less in loam and leaf-mold. As to the seedlings, 12 per cent died in watered loam and 26 per cent in watered leaf-mold to none in watered sand. In porous pots, germination was best in sand, 8 per cent less in loam, and 28 per cent less in leaf-mold. In the case of the last two, germination was 50 per cent less in painted than in porous pots. The plants in the painted sand pots remained healthy throughout the rains, while 24 per cent died in the loam and 40 per cent in the leaf-mold. When the pore-space of a soil is reduced by mechanical pressure, 25 per cent more plants may die in it during the rains than in the normal soil, while the survivors have an abnormal root-system confined to the upper, better-aerated layer. When seedlings are grown in glazed pots, some of which are corked, they become unhealthy in the open in about 10 days and eventually die, while in uncorked pots they remain healthy. Similar consequences ensue when the drainage holes are not corked, but the surface of the soil is covered with a thick layer of sal leaves.

Cannon (1915 : 64) aerated roots of *Opuntia* at 32° C. for alternate periods of 2 hours and found that the average rate of growth was 1.59 mm. for the aerated period and 1.25 mm. for the unaerated one. The increase due to aeration thus amounted to more than 25 per cent.

Free and Livingston (1915 : 60) have shown that cutting off the supply of oxygen from the roots of *Coleus* stops absorption, and this results in cessation of growth and wilting. When wilting did not go too far, the plants could be revived by renewing the access of oxygen to the soil. Cannon, and Cannon and Free, have carried out extensive investigations of root behavior under anaerobic conditions, and their results are discussed in a later section.

Butler (1919) has demonstrated that the sprouting of potatoes was retarded by reducing the oxygen-supply or by lowering the temperature to 3.7° C., and that the former was more effective in this. Respiration and consequent loss of weight were much influenced by the humidity of the air. They were also rapid in wounded potatoes during the first week of storage at 8° to 10° C. and then decreased.

Rose (1915 : 435) determined that *Martynia* and *Lactuca* gave germinations of 90 and 44 per cent respectively when treated with 80 per cent oxygen, but none when untreated. A 0.15 per cent solution of hydrogen peroxid increased the germination of *Taraxacum* from 56 to 72 per cent and that of *Datura wrightii* from 20 to 100 per cent.

Pember (1917 : 25) stated that aerating daily solutions in which barley plants were growing did not noticeably change the growth of the plants. This is explained, apparently, by the fact that the solutions were changed every 2 weeks and water added at frequent intervals to make up for water-loss.

Fred and Haas (1919 : 631) have shown that the presence of soil bacteria increases the etching power of the roots of Canada field peas. This is ascribed to the normal CO_2 excretion from the living cells of the root, together with carbonic and other acids evolved from the dead or dying root-cells broken down by bacteria.

Bergman (1920 : 13) has made a comprehensive study of the behavior of plants when their roots are submerged. When seedlings of beans, balsam, and geranium in pots were submerged in bog-water and tap-water until the top of the soil was covered, balsam began to wilt in 2 days, was badly wilted in 3 days, and beyond recovery in 4 days. The beans and geraniums began to wilt in 4 or 5 days and at the end of 5 or 6 days the leaves turned yellow and dropped. Under similar conditions *Cyperus* and *Ranunculus* grew vigorously. In a later series, air or oxygen was supplied as soon as the plants began to wilt, with the result that they regained their turgor, if not too badly wilted, and grew normally as long as aeration was continued. In 8 to 10 days all the plants developed new roots at or near the surface of the water, after which aeration was no longer needed. Balsam plants aerated by bubbling air continuously through the water in which they were submerged and by placing *Philotria* and *Spirogyra* in it, wilted not at all or but slowly in con-

trast to plants without aeration, and continued to live throughout the 3 weeks of the experiment, while the unaerated ones died. Root-hairs developed on some roots of the aerated plants. *Coleus* showed wilting in 1 or 2 days when its roots were submerged, and lost nearly all its leaves, while geranium did not show ill effects for more than a week. In the case of *Vicia faba*, plants in garden soil, peat, and *Sphagnum* with submerged roots began to wilt in 4 to 5 days.

The determination of the root-pressure of plants of *Coleus* and *Fuchsia* in soil and submerged pots showed it to be 2 to 3 times greater in the former. If the plants with submerged roots were aerated by means of bubbling air or by placing *Philotria* or *Spirogyra* in the water, the root-pressure was nearly as great and as well maintained as in the soil. The effect of submergence on the transpiration of geranium was to greatly increase it at the outset, but it quickly fell off in 2 days to a point below that in moist soil. In 2 days more the leaves began to turn yellow, and at the end of 8 days the transpiration had fallen to less than 30 per cent of the normal and in 11 days to less than 15 per cent. Seedlings of *Quercus macrocarpa* in moist and submerged soil showed similar results. Seedlings in moist soil gave a transpiration rate of 7 to 13 gm. from the second to the twenty-fourth day, while those in the submerged soil lost but 2 to 4 gm. per day.

Schley (1920 : 79) has found that the respiration of a root geotropically stimulated is greater than that of one unstimulated. The respiration-rate decreases as the time of stimulation increases.

Knudson (1920 : 379) concluded from experiments with the roots of *Pisum arvense* and *Zea* in solutions containing sucrose that the increase in reducing sugars in the latter is due to the excretion of these from the roots and not to the excretion of invertase.

Bergman (1921 : 50) has recently studied the relation between the oxygen-content and the injury of the cranberry vine due to flooding. Injury is most apt to occur during cloudy weather, when the oxygen is lowest. When submerged cranberry vines are shaded, injury results as a consequence of the reduction in the oxygen-content of the water. No essential difference was seen when the shaded vines were in pond-water or bog-water. The flowers and growing tips were most affected, owing to their higher rate of respiration and consequent greater demand for oxygen.

Summary.—The essential features of the respiration of plants were established in the short period from Ingenhousz (1779) to Saussure (1804). It was shown not only that all organs of the plant possessed this function in common, but also that roots respired in exactly the same manner as stems and leaves, in spite of the difference in medium. This is supported by practically all the evidence drawn from germination, since the early stages of this have to do with the radicle. In

consequence, there is a complete chain of evidence from Mayow (1668) to the present time as to the necessity of oxygen for root activity. The direct proof of this has been obtained by showing the use of oxygen by roots, and this has been confirmed again and again by their behavior in the absence of oxygen. It is a fact significant of the influence of the nature philosophers that the researches of Ingenhousz, Senebier, Rollo, Huber, and Saussure were followed by an almost barren period of 50 years. In spite of the experiments of Grischow, Boussingault, and a few others the labors of the earlier investigators were largely lost sight of, and their results were in a large degree to be gained anew.

The direct evidence of the necessity of oxygen for the proper functioning of roots has been furnished by Ingenhousz, Senebier, Saussure, Grischow, Garreau, Aeroboe, Vöchting, Kossowitch, Snow, Raciborski, Brizi, Day, Hunter, Hall, Brenchley and Underwood, Harrison and Aiyer, Hole and Singh, Howard and Howard, Cannon, Livingston and Free, Bergmann, and Schley. In addition to a vast amount of evidence derived from studies of germination and anaerobic respiration, the respiratory behavior of tubers, bulbs, and other underground parts affords further confirmation of that of roots. Such studies have been made chiefly upon the potato since the pioneer work of Nobbe (1865), and the investigators concerned have been Kny, Böhm, Müller-Thurgau, Mangin, Ziegenbein, Jost, Richards, Strohmer, Vöchting, Smirnoff, Grüss, Müller and Schneider-Orelli, Iraklionow, Appleman, Bartholomew, Hasselbring and Hawkins, Stewart and Mix, and Butler.

The excretion of carbon dioxid by roots was first noted by Hales (1727) and was confirmed by Ingenhousz, Saussure, Garreau, and Corenwinder, as well as by many recent observers. Its acid nature was first demonstrated by Wiegmann and Polstorf (1842) and by Oudemans and Rauwenhoff (1858). The significance of the excreted CO_2 in the economy of the soil was first suggested by Moldenhawer (1812), but was proved by Sachs's studies of the etching power exerted by roots upon rock (1860–1864), and confirmed by Knop (1861, 1864) and Cauvet (1880). Recently Fred and Haas (1919) have returned to this point to show that the presence of bacteria greatly increases the etching power of roots. Sachs had thought it possible that other organic acids might have a part in corrosion phenomena, but Stoklasa and Ernest (1905, 1908) have shown that carbonic acid alone is concerned in this under conditions that permit normal respiration.

Molisch (1887) concluded from his experiments that root excretions have both an oxidizing and reducing action, as well as a weak diastatic one. Czapek (1896) was unable to confirm the presence of a ferment, but he found that in addition to carbon dioxid, roots secreted considerable quantities of monopotassium phosphate, which

had a small share in the corrosion of rock surfaces. Raciborski (1905) has confirmed the existence of oxidizing power in the roots of a large number of plants, as have other investigators. Knudson (1920) has recently come to the conclusion that roots do not secrete invertase.

It was early shown by Saussure (1804) that the shoots of the various species exhibit different respiration intensities, and that this was true of roots as well. He found that fleshy plants required on an average but 1.1 times their volume of O, while aquatic and marsh plants needed but 1.6 times their volume, in contrast to an average of 6 times for deciduous trees and shrubs. Differences in the respiratory power of roots were also found by Garreau (1851), but the most comprehensive study was that of Freyberg and Meyer (1879), who showed that the roots of swamp plants require less oxygen than those of land plants, a fact already noted for their shoots by Böhm (1875). The respiration maximum for the roots of mature swamp plants was 78 per cent greater and for the roots of seedlings 50 per cent greater than in land plants. Hoffmann and Sokolowski, and Appleman have determined that varieties of potatoes possess different rates of respiration and exhibit corresponding differences in their relation to oxygen. The ability of roots to endure the absence of oxygen has been shown to be most variable, as indicated in the section on anaerobic respiration, and similar results have been obtained from field studies, which are discussed in the corresponding section.

AEROTROPISM.

Molisch (1884 : 111) made an exhaustive study of the growth responses of corn and pea roots to various gases and reached the following conclusions: If a growing root is exposed to a certain gas upon one side, so that the latter is present in unlike quantities for a considerable time on the two opposed sides of the root, the root departs from its normal direction of growth in a definite manner. This phenomenon is termed aerotropism. Such an effect by gases upon growing roots has been shown for oxygen, CO_2, ether, ammonia, etc. The roots are sensitive in different degrees to different gases. The effect of oxygen is weak, of CO_2 stronger, and of chlorine very strong. If a gas is too strong, the root bends towards the source of the gas (positive aerotropism); with a more moderate amount of gas it bends away (negative aerotropism). With reference to oxygen, the facts are somewhat more complex. The positive bending arises from the fact that the concave side is injured and its growth in length is less than on the opposite side. Decapitated roots react to CO_2, chlorine, and illuminating gas just as uninjured ones, though in a weaker manner.

Aerotropism is regarded as a paratonic nutation, in which the external factors influence the growing region directly, and not indirectly through the root-tip, as in hydrotropism. If young seedlings of corn are fastened so that their root-tips touch a water-surface, they show irregular bending in the water, or they turn and grow along the surface. The irregular nutations are due to abnormal influences, among them the lack of oxygen. This is confirmed by the fact that corn roots show exactly the same bendings in air lacking in oxygen or mixed with illuminating gas. The horizontal growth of the roots upon the water is an aerotropic movement determined by the high oxygen-content of the uppermost water-layer.

Goebel (1886 : 249) pointed out that the two tropical genera, *Sonneratia* and *Avicennia*, growing in swamps but not related systematically to each other, exhibit roots which grow upright. These roots were regarded as air-roots, which permitted the roots creeping in oxygen-free mud to come in contact with the air, and therefore as organs of respiration. He endeavored to test this conception experimentally, and found that upright roots developed when *Rumex*, *Nymphaea*, etc., were planted too deeply, and that similar results occurred when *Saccharum* was kept in a very wet pot. These observations confirmed the view that such roots are the result of growth processes operating under a lack of oxygen.

Jost (1887 : 601) studied the roots of a number of palms and *Pandanaceæ*, as well as those of *Saccharum*, *Cyperus*, and *Luffa*, and reached the conclusion that aerotropic roots serving as organs of respiration have a much wider distribution than has been supposed. This is shown, moreover, in greenhouses, where the roots of *Cyperus*, *Papyrus*, *Richardia*, and *Musa* appear on the upper surface of pots. It was assumed that the lack of oxygen is the stimulus which produces aerotropic roots. This is shown also by cases where roots regularly grow at the top of the pot and where they form a layer on the inner surface of the latter. *Fraxinus* and *Alnus* produce a great number of adventitious roots which run horizontally above the oxygen-free swamp soil, and such air-roots may permit trees to grow in the soil of moors. Aerotropism was considered to be widely distributed and probably to possess great biological significance.

Schenck (1889 : 526) gave the name aerenchym to a tissue developed from the phellogen of the shoots and older roots, chiefly of low shrubs growing in swamps or wet soil. It consists of thin-walled, non-suberized cells, with large communicating air-spaces much larger than the cylindric cells. It occurs in a large number of genera, *Jussiæa*, *Epilobium*, *Lythrum*, *Cuphea*, *Hypericum*, *Cleome*, *Sesbania*, etc. Most of these are shrubs, but several, *Jussiæa repens*, *J. natans*, *Epilobium hirsutum*, *Lythrum salicaria*, etc., are herbs. In a number also, *Jussiæa peruviana*, *J. pilosa*, *J. repens*, *J. natans*, are found

aerotropic rootlets with the same great air-spaces. Perseke (1877 : 27) has shown that a similar development may occur in terrestrial plants, such as *Phaseolus multiflorus*. When grown in water, the latter develops great air-spaces in the cortical parenchyma, and in roots 3 months old appear tears, due to the expansion of the air in this tissue. The aerenchym cells are in but slight contact, as in diaphragms, but the spaces are much larger. The aerenchym breaks the epidermis and cortex and its cells are then in direct contact with the medium, but the air is so firmly embedded in the tissue that water can not enter through the rifts.

The air of the aerotropic roots of *Jussiæa grandiflora* was found by Martins (1866) to contain 87.5 N and 12.5 oxygen, and that of *J. repens* to have 86.3 N and 13.7 oxygen. Immendorff determined for Schenck that the aerenchym of *Lythrum salicaria* contained 30 per cent of oxygen, and also a small quantity of CO_2. In hydrophytic shrubs without aerenchym, access of oxygen is taken care of by means of numerous lenticels, which produce in many cases a mass of stopper-cells closely resembling true aerenchym. In *Salix viminalis* the number of lenticels is much greater on submerged than on aerial shoots. The tissue contains air-spaces, is white instead of brown as in the air, and makes a plate often 2 mm. high. Similar lenticel plates are found in *Eupatorium cannabinum*, *Bidens tripartitus*, *Malachra gaudichaudiana*, *Scoparia dulcis*, *Aeschynomene sensitiva* and *hispida*, and *Solanum* sp. When *Artemisia vulgaris* grows in water, the few cortical layers of the roots develop into a tissue 2 to 3 mm. thick, and very like aerenchym, differing only in not arising from phellogen. Scott and Wager (1888) concluded that the floating tissue of the roots of *Sesbania* also facilitates the access of oxygen.

Wilson (1889) observed that the number and size of the "knees" of *Taxodium distichum* were determined by the height of the water and the duration of flooding. Young roots often turn directly upward until they reach the surface, when they again bend beneath the water. On old trees the roots often grow together and the knees arise at the point of union. In dry soil cypress trees show no trace of such development and there seems no question that they are to be regarded as aerating organs. Similar structures are found about the base of trunks of *Nyssa aquatica* in swamps, the roots bending sharply upward to a distance of 6 to 8 inches above the surface of the water and then bending downward into it again.

Ewart (1894 : 238) found that, when peas were suspended above water free from oxygen with the radicles touching, the radicles that pointed downward soon bent laterally or curved sharply upwards, while those pointed upward grew in that direction for a longer period than usual before responding to geotropism. When they reached the water they bent upward or grew along over the surface. Over

well-aerated water, peas grew downward, regardless of their original position. When the aeration was stopped, growth ceased or went on but slowly. If the stagnant oxygenless water was aerated, the radicles grew downward into it, in spite of the carbon dioxid in it, thus indicating that the previous curvature was a response to oxygen. In consequence, the term oxytropic was proposed for this type of irritability. Similar experiments with hemp and wheat gave the same results, though hemp showed less marked response.

Later studies (1896 : 191) with seedlings of hemp and peas in tubes filled witht boiled sterilized water and closed with a plug of cotton confirmed the existence of oxytropic curvature. The primary roots of sunflower were strongly oxytropic, the secondary ones but slightly so, while the radicles of *Cucurbita* showed distinct oxytropism. Wieler (1898) has studied the pneumatodes of *Phœnix* and *Chamærops* and finds that in some respects they correspond to the aerenchym of Schenck, but he was unable to find any proof that they were definitely related to aeration.

Pfeffer (1900 : 182) stated that oxytropic reactions are feeble and that it is yet to be shown that they play a prominent part in the orientation of roots in water and soil. He also regarded it as uncertain whether the upward growth of roots in mud or water-logged soil is due to oxytropism or to an alteration of geotropic irritability produced by the deficiency of oxygen. The absence of oxygen produces disturbances of growth which often result in irregular curvatures. When curvature is toward the region with more oxygen, growth is more rapid. It appears, however, as though the avoidance of regions poor in oxygen is in part aided by the suppression or reversal of the geotropic irritability, for on repeating Ewart's experiments on a klinostat he was unable to obtain constant and definite curvatures away from the deoxygenated region.

Bennett (1904 : 241) repeated Molisch's studies of the behavior of roots to different gases, employing his methods, and came to the conclusion that the curvatures noted were due to hydrotropism. In further experiments, roots of *Zea mays*, *Pisum sativum*, *Raphanus sativus*, *Cucurbita pepo*, and *Lupinus albus* were subjected to one-sided access of oxygen, hydrogen, and carbon dioxid to determine the presence of aerotropism. When the roots were grown in water between submerged chambers containing air on one side and CO_2 or H on the other, no constant or regular curvatures occurred, as was also true when they were placed in a similar position in a damp chamber. Similar results were obtained when the roots were grown in a thin vertical layer of earth separating air and CO_2 or air and hydrogen, or in earth with air on one side and carbon dioxid or hydrogen on the other, or in gelatin under similar disposition of the air and gases. The conclusion is reached that, in so far as the representative land plants used were concerned, definite curvatures are

not produced in roots by the one-sided access of such gases as oxygen, hydrogen, or carbon dioxid, and their roots are therefore not aerotropic. The evidence is regarded as being decidedly against a belief in the aerotropism of roots.

Sammet (1905 : 621), at the suggestion of Pfeffer, has investigated the degree to which roots in water, roots in earth, and roots, shoots, and fungal hyphæ in saturated air respond to the unequal distribution of various substances. In saturated air the roots responded in different ways. To oxygen they reacted only by positive curvature, while to carbon dioxid, ether, etc., higher concentrations gave positive and lower, negative curvatures. A stream of air produced no reaction in completely saturated air, but in air somewhat less than saturated, hydrotropic curvature occurred. The roots in soil showed combinations of chemotropism and hydrotropism, but when oxygen was applied to the surface of dry soil, the roots curved upward to the surface, showing that aerotropism was stronger than the influence of hydrotropism. Intact and decapitated roots showed the same behavior to chemotropic stimuli, but hydrotropic response was suppressed in the latter.

Bergmann (1920 : 16) found that, a week or so after the submergence of roots in water, new laterals appeared on the base of the stem at the surface of the water. An examination showed that the submerged roots had died. In the case of plants in soil wet from below, the upper roots made the greatest growth; the lower ones remained alive in *Impatiens*, but died in *Pelargonium*. Cannon and Free (1920:62) have found that the roots of sunflower behave similarly when placed in an atmosphere of nitrogen.

Summary.—In spite of the conclusions of Bennett and the confirmation given by the experiment of Schreiner and Reed (1903), the evidence in support of the aerotropic curvature and growth of roots is practically conclusive. While Bennett has succeeded in throwing doubt upon Molisch's results, her own conclusions are too sweeping, owing to the failure to reckon with the oxygen already in the roots of the media used. Most of the experiments were carried on for too brief a period, 10 to 30 hours as a rule, and no account was taken of the inhibiting effect of the amount of the gases used. Molisch, Goebel, Ewart, and Sammet have furnished the experimental evidence of aerotropism or oxytropism, while Goebel, Jost, Schenck, and Wilson have observed aerotropic effects in the plants of swamps especially.

In connection with the comprehensive study of bog and swamp vegetation, preliminary experiments have been made upon the behavior of roots in saturated soil. In three successive series of pot experiments, seeds of sunflower and bean were planted in various positions in glazed pots filled with sandy loam. In two of these an

unglazed area 2 inches square was left on the opposite side; in others the unglazed area was a zone; while in others all water was added from the bottom. After 2 days the pots with unglazed areas for the access of air were sealed by pouring the usual wax over the surface of the soil. After a period varying from 3 to 5 days in the different series, the soil-mass was carefully removed from the pots in such a way as to preserve the relation to the unglazed area. In all cases the bean seeds were found to have decayed without germinating and sunflower alone was used in the remaining series. Even the sunflower failed to germinate in the soils constantly saturated from below. The two pots with the unglazed square gave positive curvatures toward this area in all three series, though this was less true of those with the unglazed zone, owing to the more general diffusion of the air. In the former, all the seedlings showed right-angled curvatures toward the direction of air access, without a single negative or opposite response.

AIR OF SOIL AND PLANTS.

AIR-CONTENT OF THE SOIL.

Earlier researches.—Boussingault and Lewy (1853 : 5) were the first to determine the composition of the air contained in the soil. They analyzed the air-content of various soils, namely, soil recently manured, soil of a field of carrots, soil of a vineyard, forest soil, sandy soil, humus soil, bed of asparagus, beet field, field of alfalfa, etc. The highest amount of carbon dioxid, 3.83 per cent, was found in the soil containing abundant humus, and conversely, the smallest amount of oxygen, 16.43 per cent. Soil recently manured yielded 2.17 to 2.25 per cent of carbon dioxid, but after frequent rains this had increased to 9.74 per cent and the oxygen had decreased to 10.35 per cent. Sand contained the smallest amount of CO_2, 0.11 to 0.19 per cent, and the largest amount of oxygen, over 20 per cent. They found the average amount of CO_2 in soils not fertilized for a year to be 22 times the amount in normal air, while in manured soils the amount was 245 times greater. They concluded that the greater part of the carbon dioxid is derived from the oxidation of organic matter in the soil, and that a small but constant part of the oxygen combines with the hydrogen derived from fermentation.

Petenkoffer (1871 : 395) determined the amount of carbon dioxid in the soil-air at Munich from September 1870 to November 1871. Samples were taken at 0.66, 01.5, 2.5, 3, and 4 meters. He found that the air of the upper soil-layers contained less carbon dioxid from August to June, and more throughout June and July. At 1.5 meters the amount rose from 0.26 per cent in January to about 0.8 per cent in July, and reached its maximum at about 1 per cent in August to fall to 0.5 per cent in November. At 4 meters the amount rose

from 0.35 per cent in January to 0.6 per cent in July, reached its maximum at over 1.5 per cent in August and fell to 0.6 per cent in November. Another series of determinations (1873 : 250) of the CO_2 content of soil-air at Munich at depths of 1.5 and 4 meters was made from November 2, 1871, to November 29, 1873. It was found as before that the CO_2 was greater at the greater depth, and in midsummer sometimes twice or nearly thrice as much. The mean for July was 0.26 per cent at 4 meters and for January, 0.05 per cent. The author also gave the results of Fleck's observations at 2 meters, 4 meters, and 6 meters in Dresden. The soil of the botanic garden in Dresden contained several times as much CO_2 as the Munich soil studied.

Risler (1872; cf. Mangin, 1896) studied the variation in CO_2 in soil at depths of 0.25 meter and 1 meter in relation to both temperature and weather. He found the maximum amount, 2 per cent, present late in June, as well as a greater amount always at the lower depths.

Fleck (1872; cf. Pettenkoffer, 1873) found the intensity of the decomposition process in the soil and the amount of CO_2 determined by mechanical pressure, size of particles, and the water-content. Garden soil without a plant cover showed more CO_2 in the lower layer, while that covered with plants gave the largest amount in the upper layer, as also did sandy soil covered with forest. The total amounts in the latter were usually less than one-tenth those of the garden soil.

Table 5.

Soil-air of garden soil.						Soil-air of a sandhill covered with forest.		
2 meters.		4 meters.		6 meters.		2 meters.	4 meters.	6 meters.
CO_2	O	CO_2	O	CO_2	O	CO_2	CO_2	CO_2
p. ct.	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*
1.68	18.9	2.75	17.3	3.38	16.7	0.47	0.42	0.34
2.42	18.1	3.59	17.0	3.63	17.0	0.56	0.51	0.21
2.89	16.3	4.00	15.7	4.52	14.9	0.75	0.64	0.52
4.82	16.2	5.56	16.8	6.33	14.8	0.79	0.66	0.58
.....	.....	4.98	16.2	6.36	14.8	0.51	0.52	0.47
2.91	18.6	4.60	15.6	6.11	14.9	0.36	0.35	0.34
2.21	19.7	4.32	16.7	7.96	13.6	0.22	0.28	0.29

Schloessing (1873 : 203) studied the intensity of oxidation in a calcareous soil containing different amounts of oxygen, namely, 1.5, 6, 11, 16, and 21 per cent. The oxidation was considerably less in the first, identical in the next three and somewhat greater in the last. He later (1889 : 673) determined the composition of the soil-air at 15 to 65 cm. of depth and at various places and times during the growing-season. The amount of CO_2 varied widely from 0.5 per cent to 11 per cent, and the oxygen from 10 per cent to 21 per

cent. There was a general tendency for the carbon dioxid to increase with the depth, but this was not absolute. Habitats at the base of a slope tended to have more CO_2 than those higher up.

Smolenski (1877 : 383) concluded that the degree of contamination of the soil is a predominant factor in the amount of CO_2. For example, while he found from 0.1 per cent to 2 per cent in ordinary soil, the amount rose to 10.2 per cent in contaminated soil. Renk (1878) confirmed the results obtained at Munich by Pettenkoffer.

Möller (1878 : 121) summarized his results from the study of soil-air as follows: The air in purely mineral soil or in absolutely dry soil contains no more carbon dioxid than the atmosphere. Soils with organic constituents possess a constant source of carbon dioxid. The formation of carbon dioxid shows but slight variations when the external conditions are the same. Soil may become so dry that the production of carbon dioxid ceases. On the other hand, a very small amount of water suffices to bring about the production of the same amount of carbon dioxid as when it is saturated. When an air-dry soil is abundantly watered, there results a considerable but temporary increase in the carbon-dioxid content. In a later paper (1879 : 329), a comparative study was made of the carbon dioxid in fallow and cultivated fields and in several kinds of soil. The cultivated field regularly showed 5 to 6 times as much carbon dioxid as the fallow field, while calcareous soil contained as a rule considerably more carbon dioxid than clay, and both these soils several times as much as sand.

Audoynaud and Chauzit (1879) obtained somewhat different results from those of Boussingault and Lewy in regard to the composition of soil-air, as shown in table 6.

TABLE 6.

	1876			Time.	1879	
	I	II	III		CO_2 and O	N
	p. ct.	*p. ct.*	*p. ct.*		*p. ct.*	*p. ct.*
CO_2...	4.5	1.65	3.4	1. August	14.5	85.5
O.....	8.9	11.59	10.3	4. August	12.9	87.1
N....	86.6	86.79	86.3	5. August	15.5	84.5
				6. August	17.1	82.9
				7. August	17.7	82.3

The soil-air was much richer in nitrogen and poorer in oxygen than in the studies of Boussingault and Lewy. The authors assumed that the decrease of the oxygen was due not alone to its use in respiration or oxidation in the soil, but also to the different osmotic relation of nitrogen and oxygen in the passage through the soil.

Fodor (1881) found that the amount of CO_2 in soil-air was very variable, the maximum being 14.3 per cent. He concluded that

there was no relation between the amount of CO_2 and of organic matter found in the soil, and that the former depends primarily upon permeability. The soil-air contained more carbon dioxid and less oxygen at 4 meters than at 1 meter.

TABLE 7.

	1 meter.	4 meters.	3 meters.
	p. ct.	*p. ct.*	*p. ct.*
CO_2....	0.89 to 1.03	2.6 to 5.4	.....
O	18.79 to 21.33	.....	17.29 to 18.53

Salger (1882) confirmed the previous results as to the increase of CO_2, and found the amount greater at great depths, such as 20 meters. Further, the amount increased with the contamination of the soil, while regular ventilation diminished it rapidly in the surface layers, but more slowly than at greater depths. Contrary to the usual results, Bentzen (1882 : 446) stated that the atmosphere of the upper layers was richer in CO_2 than that of the lower.

Ebermeyer (1878 : 158) determined the amount of carbon dioxid in soil-air with particular reference to the difference in this respect between forest and field soils. His results for the four summer months, May to August, are given in Table 8.

TABLE 8.

	p. ct.		*p. ct.*
Bare, unfertilized, unworked soil at 1 meter.....	2.3	Forest soil in the humus layer.....	0.14
Same soil under an Acacia.....	1.4	Forest soil at 0.5 meters.....	0.45
Free air 2 meters above the soil.....	0.04	Forest soil at 1 meter.....	0.5
Forest air 2 meters above the soil ...	0.08	Soil of cultivated field at 0.5 meter..	2.6
		Soil of cultivated field at 1 meter....	2.5

He concluded that forest air contains twice as much carbon dioxid in summer as free air and that forest soil is much poorer in CO_2 than unforested soil, while a cultivated field contains 5 to 6 times as much. With an increase of temperature, the CO_2-content of the cultivated field increases more rapidly than that of the forest soil. The movement of CO_2 in the soil seems to be very slow, as shown by the difference in amount in contiguous places in the soil.

He also (1890 : 15) found that the air in mineral soil is always richer in CO_2 and poorer in oyxgen than ordinary air. The soil-air in the upper layers was 4 to 5 times richer, and at 70 cm. deep, 10 to 20 times richer in CO_2 than the atmosphere. Among the soils, quartz sand was poorest in carbon dioxid, while calcareous sand and clay were at least once again as rich. Dry moor soil was far richer in CO_2 than the pure mineral soils. This was true in the uppermost layers, but especially at 70 cm. deep, where it was 22 times greater than in sand and 10 times greater than in lime and clay soils. In

forested soil, the soil-air was much poorer in CO_2 than that in neighboring manured or humus fields. The CO_2-content of the soil-air stands in a definite relation to the chemical activity of the soil, and constitutes a definite measure of the latter. Under similar conditions the CO_2-content of the soil-air in deep beech forests during the growing-season is only about half that of a pine forest of equal age. The CO_2-content of the soil-air is always less in closed forests than in cultivated fields or in open bare soil. Soil-air is, as a rule, poorer in oxygen as it is richer in CO_2. Humus and calcareous soils in bare situations are more active, richer in CO_2, and poorer in oxygen than all other bare soils. They even exceed dry moor-soil in this respect. A living cover reduces decomposition and the production of carbon dioxid.

Wollny (1880 : 1373) studied the effect of plant cover and shade upon the amount of carbon dioxid in the soil-air and reached the following conclusions: Soil covered with living plants contained less carbon dioxid than fallow soil or mulched soil during the warmer half of the year, the respective amounts being 0.19, 0.88, and 0.67 per cent. During the colder half, the soil beneath the grass cover contained more carbon dioxid in the ratio of about 2 to 1, the amount being only about one-third as much as in the summer. The amount of carbon dioxid increased more rapidly in fallow or mulched soil with rising temperatures than in that with a plant cover. With the increase of rainfall the amount of carbon dioxid increased several times in cultivated soil and fell in bare soil or soil mulched with straw. The soil under a cover of living plants was poorer in carbon dioxid in proportion to the density of the plants, owing to the reduced water-content and the lower temperature resulting from the shade. He also found that the CO_2 content under similar conditions rises and falls in general with the amount of organic material in the soil. The atmospheric air is materially concerned in the formation of CO_2 in the soil. This is not completely prevented by the removal of the air through one of the gases not concerned in the decomposition of organic material. Carbon dioxid is also formed in the soil through the agency of lower organisms.

Wollny (1886 : 165) investigated the influence of the physical properties of the soil on the amount of CO_2 in it. He found the latter to be greatest at a certain slope (20°), while it decreased both with less slope (10°), or a steeper one (30°). As to exposure, on an average the south slopes were the richest and the north the poorest in CO_2, while the latter was intermediate on east and west slopes. With reference to the color of the soil, the dark-colored soils were poorer in CO_2 than the lighter ones. This was true, however, only under dry conditions, for, when the water-content of the two soils was the same, the darker contained more CO_2. The CO_2-content of the soil under like amounts of organic material was the greater

the finer the particles. Carbon dioxid increased with the depth of the soil layer. A soil shaded by living plants contained during the warm season a smaller amount of CO_2 than a fallow soil, and this again less than one covered with a layer of dead plant material. In the last case the amount of CO_2 increased with the thickness of the layer. It was also found (1889 : 385) that the soil in bright, warm, and dry weather is the richer and in cloudy, cool, and moist weather the poorer in CO_2 under conditions otherwise similar, the darker the color of the surface.

Wollny (1890) summarized his results upon the influence of organic matter as follows: The amount of CO_2 in the soil-air is proportional to the amount of organic material present only when this is small. The production of CO_2 with a high content of the soil in organic material increases in smaller degree than the amount of organic material, or remains the same, because at a higher CO_2-content the activity of the organisms of decomposition is limited, and with the increase of the organic material above a certain limit the properties of the soil most important for decomposition are changed in a fashion unfavorable for the intensity of the process. The amount of CO_2 present in the soil gives neither a measure of the intensity of organic processes nor of the amount of humus material present. In a later study (1896 : 151) it was shown that soil covered with plants possesses a higher content of CO_2 than bare soil under conditions otherwise similar. The reverse is true when the bare land is manured. The soil-air in soil covered with grass or with birches is richer in CO_2 than one covered with pine. The soil under the pines without a covering of straw contains larger amounts of CO_2 than one with a straw cover.

Mangin (1895 : 1065) analyzed the soil-air for the purpose of determining the cause of retardation in the leafing of *Ailanthus* and *Ulmus* at Paris. In the case of *Ailanthus* with open buds, he found the CO_2-content of the soil to range from 0.35 to 3.43, with the average at about 1.5 per cent, while in *Ailanthus*, with buds still closed, it varied from 3.89 to 24.84, the average being about 10 per cent. The oxygen in the first case ranged from 17.86 to 20.3 per cent, with an average of about 19 per cent, and in the second from 31.6 to 15.92 per cent, the average about 10 per cent. In the case of elms with normal leafing, the carbon dioxid varied from 0.67 to 2.12 per cent, the average being about 1 per cent, while those with leafing retarded 15 to 20 days showed a range of 1.71 to 5.81 per cent, with the average about 3 per cent. Similarly, the oxygen ranged from 17.86 to 20.05 per cent, and from 6.26 to 17.72 per cent, the average being about 14 per cent.

Later researches.—Letts and Blake (1900 : 213) have made a comprehensive summary of the results of Pettenkoffer, Fodor, Wollny, and others with respect to soil-air. This results from atmospheric

air diffused into the soil and changed by loss of oxygen and considerable increase of CO_2. The sum of these two, however, is not very different from the original proportion of oxygen. More CO_2 is found at lower than at higher soil-levels. The amount increases during spring and summer, diminishes after August, and remains more or less stationary during the winter months, the variations being due to temperature changes. The amount of CO_2 in the soil-air, depends upon its porosity and its organic matter, the relation being inverse in the first and direct in the second. Rainfall has a marked influence on the CO_2 of the soil-air.

Stoklasa and Ernest (1905 : 723) have shown that the CO_2-content of the soil-air is derived either from the respiration processes of micro-organisms, especially bacteria, molds, and algæ, or the respiration of the root-systems of plants. With greatly limited access of air, decomposition begins, as a consequence of which the mineralization of the organic materials takes place much more slowly. Proof that the source of the CO_2 is not in the chemical processes, but in the activity of the micro-organisms, is afforded by the fact that no development of CO_2 is noticed when the soil is sterilized or the organisms destroyed by antiseptics.

Lau (1906 : 33) reached the following conclusions as a consequence of his study of the air in the soil: Soil-air is richest in CO_2 in summer, next in autumn, then in spring, and least in winter. The maximum occurs in the months of July and August, the minimum in February. The CO_2-content of soil-air increases with the depth. Soil-air is poorest in CO_2 in sand, intermediate in clay, and richest in moor-soil. It is poorer in oxygen as it is richer in CO_2. At the same depth the soil-air is richer in CO_2 at the root-level in a cultivated field than in a bare one. It is richer in CO_2 in the root-layer than beneath it. The amount of carbon dioxid increases with the greater development of plants and increasing soil-temperature. Soil-air is richer in CO_2 in soil containing potatoes or lupines, which respire intensively, than in soil with oats or barley, which respire weakly. Soil-air is poorer in CO_2 about 2 a. m. than it is at 2. p. m. It is richer in sandy soils manured with organic material than in those unfertilized. The soil-air in unfertilized lupine beds is but little poorer in CO_2 than in fertilized ones.

Vageler (1907 : 19) has made a comprehensive study of the soil-air of various moor communities. A large number of analyses of the soil-air of moors shows that the greatest amount of CO_2 and the least oxygen occurs in the *Molinietum*, namely, 2.68 per cent and 16.68 per cent, while the *Arundinetum*, for example, has 0.13 per cent of CO_2 and 20.23 per cent oxygen. The carbon dioxid in the moor-soil is an ecological factor in so far as its amount furnishes a measure of the decomposition processes in the soil, modified through the higher or lower air-content of the rhizosphere and the nature of the soil

material. A high content of CO_2 in the soil-air is identical with a high degree of activity of the soil, and this, with the ability to bear a flora of high requirement. A poisonous effect from soil-air with a few per cent of CO_2 was nowhere found in the moor. It is regarded as probable that it does not occur until the amount reaches such as those which Mangin found in Paris.

Jodidi and Wells (1911 : 146) measured the amount of carbon dioxid and oxygen in the soil of 22 field plots during the months of April, May, June, July, and August. The averages for each month are shown in table 9.

TABLE 9.

Time.	CO_2	O
	p. ct.	*p. ct.*
April.....	0.191	20.93
May.....	0.182	20.60
June.....	0.299	20.37
July.....	0.256	20.39
August.....	0.344	20.30

The oxygen-content of the various plots varied little more than 1 per cent throughout the period, but the carbon dioxid showed a maximum range from 0.04 per cent to 0.82 per cent. This bore little relation to the previous treatment of the plots, as plots A and C, with the same treatment for the preceding 4 years, gave values of 0.10 and 0.82 per cent respectively during the month of June.

Harrison and Aiyer (1913) have determined the composition of the gases from rice fields in India under various treatments and shown that manure greatly increases the production of CO_2.

TABLE 10.

Gas derived from—	Year.	CH_4	N	CO_2	O	H
		p. ct.	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*
Cropped manured plot.....	1909	21.0 to 74.0	11.0 to 73.0	4.5 to 14.6	0.0 to 2.8	.....
	1910	17.0 to 71.0	11.0 to 78.2	2.0 to 21.0	0.0 to 1.9	0.0 to 1.2
	1911	16.6 to 66.1	15.8 to 78.8	1.4 to 6.6	0.0 to 1.9	9.0 to 11.3
Uncropped unmanured plots....	1911	26.4 to 57.2	39.9 to 66.4	1.4 to 5.1	0.0 to 5.7	0.0 to 6.3
Cropped unmanured plot	1911	0.0 to 53.8	41.9 to 96.8	1.3 to 5.9	0.0 to 1.4	0.0 to 3.1

Leather (1915 : 108) has made a comprehensive study of the gases in the soils of fields with different treatments. In unmanured fallow land in the spring of 1907, the amount of oxygen varied from 17.2 per cent at 3 to 6 inches to 15.5 per cent at 6 feet, the maximum being 18.6 per cent at 9 to 12 inches and the minimum 13.4 at 5 feet. The carbon dioxid ranged from a minimum of 2.9 per cent at 3 to 6 inches

to 8.2 per cent at 6 feet, the maximum being 8.5 per cent at 1 and 5 feet approximately. In manured land in October, the oxygen was 11.4 and 13.2 per cent, and the carbon dioxid 1.98 and 5 per cent at 9 to 12 and 29 to 30 inches respectively. In December, the oxygen was 14.7, 14.7, 13.6, and 17.8, and the carbon dioxid 6.8, 4, 10, and 4.3 per cent at 9 to 12, 19 to 20, 29 to 30, and 40 to 43 inches respectively. Fallow land after green-manuring gave a range of 10 to 12.5 per cent of oxygen at various depths, and of 3.5 to 10.1 per cent of carbon dioxid with one crop and a maximum of 18.4 per cent with another. The gas from swamp rice-land yielded the following averages: nitrogen, 85.57 per cent; oxygen, 0.54 per cent; carbon dioxid, 4.42 per cent; hydrogen, 5.75 per cent; methane, 2.81 per cent; argon, 0.893 per cent. The amount of oxygen in soil at various depths up to 15 inches about the roots of *Crotolaria juncea* ranged from 2.23 to 9 per cent, and the CO_2 from 4.84 to 16.99 per cent; about the roots of *Indigofera arrecta*, the respective ranges were 3.33 to 5.24 per cent and 12.62 to 21.14 per cent, and about those of *Zea mays*, 6.28 to 13.82 per cent and 3.34 to 12.30 per cent. The amount of oxygen in fallow land decreased about 1 per cent after nitrification, and the carbon dioxid increased slightly, while nitrification in vessels usually reduced the oxygen from 20.93 per cent to less than 1 per cent, and resulted in the production of 12 to 24 per cent of carbon dioxid. The outstanding results are the relatively low content of oxygen and high carbon-dioxid content about the roots of plants, and the great amounts of oxygen used and carbon dioxid evolved in nitrification.

Russell and Appleyard (1915 : 1) have studied the free air of Rothamsted soils and found that to a depth of 6 inches it differs from atmospheric air in containing about 10 times as much carbon dioxid, namely, 0.25, in contrast to 0.03 per cent, and practically the same amount of oxygen, 20.6, as against 20.96 per cent. During rapid nitrification there is a perceptible falling-off of oxygen and a still greater one in water-logged soils. The air dissolved in the water and the colloids of the soils consists chiefly of carbon dioxid and nitrogen, and contains practically no oxygen. Variations in the composition of the free air arise mainly from fluctuations in the chemical processes of the soil, the curves following those of the amount of nitrate and the bacterial counts. Weather conditions appear to have little effect upon the soil-air, and no evidence was obtained that growing crops greatly increase the carbon dioxid in it. The dissolved oxygen brought in by rainfall is a factor of considerable importance in renewing the soil-air and facilitating chemical change.

Hole and Singh (1916) find that when rain-water with an initial content of 1 mg. of carbon dioxid and 7 mg. of oxygen was kept in contact with the loam of a sal forest, the oxygen fell to 1 mg. and the CO_2 rose to 60 to 70 mg. in 2 days, and then to 230 mg. in 28 days.

As no plants were growing in the soil, this effect was due to the living soil organisms.

Howard and Howard (1920) give in table 11 the results obtained by Mukherjee in determining the amount of CO_2 in three plots with different treatment.

TABLE 11.

Month.	1. Grassed down.	2. Grassed down but partially aerated by trenches.	3. Surface cultivated.
	p. ct.	*p. ct.*	*p. ct.*
January	0.444	0.312	0.269
February	0.472	0.320	0.253
March	0.427	0.223	0.197
April	0.454	0.262	0.203
May	0.271	0.257	0.133
June	0.341	0.274	0.249
July	1.540	1.090	0.304
August	1.590	0.836	0.401
September	1.908	0.931	0.450
October	1.297	0.602	0.365
November	0.853	0.456	0.261

Summary.—The amount of carbon dioxid regularly increases with the depth of the soil, and the amount of oxygen decreases correspondingly. Since the carbon dioxid is derived from respiration and decomposition in the soil, it is most abundant in soils and at depths where its escape into the air is most difficult. On the other hand, the supply of soil-oxygen is obtained from the air, and the amount decreases with the distance from the source and the increasing tribute taken by the roots. The complementary nature of the two gases in the soil is a direct result of the respiration ratio. Pettenkoffer (1871) was the first to determine that the amount of carbon dioxid was greater with the depth, and that in midsummer it was 2 or 3 times as much at 4 meters as at 1.5 meters. Similar results were obtained by Fleck (1872), Risler (1872), Salger (1882), Schloessing (1889), Ebermeyer (1890), Lau (1906), and Leather (1915), the results of the last two being especially detailed and complete. Fleck showed that the reverse relation existed in sand, and this probably furnishes the explanation of Bentzen's view that carbon dioxid was more abundant in the upper layers.

Seasonal changes, especially temperature and rainfall, have a marked influence upon the composition of the soil-air, though part of this is often to be ascribed to the effect of vegetation. Pettenkoffer found that the carbon dioxid was least abundant in January and most abundant in August, the ratio being about 1 : 4. Risler obtained the maximum amount late in June, while in Lau's studies it fell in July and August and the minimum in February. The lat-

ter also showed that soil-air is richest in CO_2 in the summer, less so in autumn, still less in spring, and least in winter. For the growing-season, Jodidi and Wells (1911) found the smallest amount of carbon dioxid in May and the largest in August. In India, the minimum occurred in May and the maximum in September, the ratio being 1 : 7 (Howard and Howard, 1920).

As would be expected, sand contains the least carbon dioxid and the most oxygen. This was early shown by Boussingault and Lewy (1853), who found 0.11 to 0.19 per cent of CO_2 and over 20 per cent of oxygen in sand, while Fleck showed that the soil-air of sand contained about one-fourth as much carbon dioxid at 2 meters as garden soil, and about one-tenth as much at 6 meters. Möller (1878) obtained considerably more CO_2 from calcareous soil than from clay, and several times as much from both as from sand, while Ebermeyer's results showed quartz sand poorest in CO_2, calcareous sand and clay twice as rich, and dry moor-soil far richer. Lau likewise determined that sand was poorest, clay intermediate, and moor-soil richest in carbon dioxid.

The general effect of organic matter and manure is to greatly increase the amount of carbon dioxid and to decrease the oxygen. The most CO_2 and the least oxygen were found by Boussingault and Lewy in soils containing abundant humus, and in those recently manured. The latter yielded 10 times as much CO_2 as soils not fertilized for a year. Smolenski (1877) obtained from 5 to 100 times as much carbon dioxid in contaminated as in ordinary soil, and Salger confirmed his general results. Wollny (1880) determined that the amount of carbon dioxid in the soil rose and fell in general with that of organic material, but the amounts were proportional only when the organic matter was not too abundant. Lau found that organic material increased the production of CO_2, while Jodidi and Wells found little relation to previous differences of treatment. Harrison and Aiyer (1913) obtained as much as 14 to 21 per cent of carbon dioxid from manured plots, while Leather observed a maximum of 18 per cent in fallow land after green-manuring.

Cultivation and plant-growth generally augment the carbon dioxid of the soil-air and diminish the oxygen in proportion. Möller showed that the soil of cultivated fields regularly contained 5 to 6 times as much carbon dioxid as that of fallow fields, while Fleck observed that in a soil covered with plants, carbon dioxid was most abundant in the upper layers. On the other hand, Ebermeyer concluded that a living cover reduced decomposition and the consequent production of CO_2. He found forest-soil much poorer in carbon dioxid than unforested, and 5 to 6 times poorer than cultivated soil. The soil-air of a deep beech forest contained but half as much carbon dioxid as that of a pine forest. Wollny's results as to the effect of a living cover appear somewhat contradictory, but his final

conclusion (1896) was that soil covered with plants possesses a higher content of CO_2 than bare soil under conditions otherwise similar. The composition of the soil-air varies with the plant cover concerned, as would be expected. Lau stated that the soil-air contains more carbon dioxid at the root-level in a cultivated field than in a bare one, and that there is more in the root-layer than beneath it. The carbon dioxid increases with the greater development of plants, and also varies with the kind of plant. The effect of plants upon the composition of the soil-air is most graphically shown by the results of Leather, who found minimum amounts of 2 to 6 per cent of oxygen and maximum amounts of 12 to 21 per cent of CO_2 about the roots of crop plants in India. The results obtained by Howard and Howard indicate that the amount of carbon dioxid is usually 2 to 4 times as great in grass plots as in those with the surface cultivated.

While investigators have differed much as to the importance of the various factors in modifying the composition of the soil-air, it seems evident that this depends in the first place upon the intensity of respiration and oxidation in the soil and secondly upon the possibility of diffusion through it. The soil having the largest amount of living organisms in it will consume the most oxygen and produce the most carbon dioxid. Since many of the most active organisms are microscopic, cursory observation is insufficient to determine the actual importance of a plant cover or the presence of organic matter. In addition to the flowering plants, ferns, mosses, and larger fungi which may constitute the visible cover are a host of microscopic fungi, molds, bacteria, and algæ, together with soil animals from amœbæ to rodents. All of these have a larger or smaller part in increasing the CO_2 and decreasing the oxygen of the soil, but the algæ may reverse this process under conditions permitting photosynthesis. Any factor that promotes respiration or oxidation, such as higher temperature or water-content, will increase the carbon dioxid at the expense of the oxygen, and those that retard respiration will have the opposite effect. The amount of organic material in the form of humus, manure, or green manure is naturally of great importance as a source of energy for molds, bacteria, protozoa, etc. The porosity of the soil is directly important in determining the rate at which oxygen can enter and carbon dioxid escape and indirectly in that it affects the water-content, temperature, organic matter, and number of organisms.

Since water contains but 6 to 7 c.c. of oxygen per liter when saturated during the growing season, the water-content and air-content of the soil stand in inverse relation to each other, in so far as respiration is concerned at least. The greater the water-content, the smaller the air-content and the amount of available oxygen, and the reverse. Dry soils contain relatively large amounts of air, and wet soils little air, regardless of their fineness. Under the same rain-

fall, porous soils have a larger air-content than fine or compact ones, and this is true even when they approach saturation, owing to the readier movement of water in them. Water-logging is practically confined to heavy soils, and swamps are typical of alluvium. Saturated soils contain air only in solution, and the amount available is sufficient only for water-plants, which possess some device for aeration in the case of helophytes and plotophytes. As many investigators have shown, land-plants, with the rarest exceptions, fail to find enough oxygen in saturated or water-logged soils, and die as a consequence.

As shown in a following section, the amount of carbon dioxid necessary to produce injury ranges from 2 to 20 per cent, depending upon the plant. Such percentages are far from infrequent, especially in manured and water-logged soils. Boussingault and Lewy found 9.74 per cent in manured soil wet by frequent rains, while Fleck obtained 7.96 per cent in garden soil, and Smolenski 10.2 per cent in soil that had been contaminated. Mangin determined that amounts of carbon dioxid ranging from 3.89 to 24.84 per cent were sufficient to retard the leafing of *Ailanthus*, the higher percentages being fatal to the trees. The elm was much more sensitive, retardation occurring from 1.71 to 5.81 per cent. Harrison and Aiyer found maxima ranging from 6.6 to 21 per cent in the gas of cropped and manured rice plots. Leather obtained maxima of 10.1 and 18.4 per cent in fallow fields after green manuring, and of 12.30, 16.99, and 21.14 per cent about the roots of plants. These results make it practically certain that injury from CO_2 is much more frequent than is commonly supposed, especially in field and garden soils that have been manured, and indicate that it must be taken into account in all cases of toxic action.

AIR-CONTENT OF WATER.

Morren and Morren (1841 : 9) determined the composition of the gas of a vivarium 20 feet in each direction, following the changes throughout the growing-season from March to September. They found that the CO_2 varied from 1.27 per cent to 23.04 per cent, and often very rapidly, these two extremes occurring on the 9th and the 19th of August. This maximum amount of CO_2 led to the death of small animals and finally to that of the fishes. The amount of oxygen varied from 18.01 per cent to 60.43 per cent, the close relation to the CO_2 being shown by the fact that the maximum occurred on August 9 and the minimum on August 19, the dates for the minimum and maximum of CO_2.

Whipple and Parker (1902 : 104) have given a comprehensive series of tables of oxygen and carbon dioxid in dealing with the effect of gases on microscopic organisms. At 20° C., 1 liter of water can absorb 28 c.c. of oxygen, 14 c.c. of nitrogen, and 901 c.c. of carbon

dioxid. The amount of oxygen in distilled water when saturated varies from 9.7 c.c. per liter at 0° C. to 7.77 c.c. at 10° C., 6.28 c.c. at 20° C., and 5.43 c.c. at 30° C. Hence the amount of oxygen in water varies from about 9 c.c. in midwinter to 6 c.c. in midsummer. Ponds and reservoirs in Massachusetts often showed 100 per cent of saturation at the surface and at 10 and even 20 feet, ranging usually to zero at 40 to 50 feet. River-water in Ohio ranged for the most part from about 80 to 100 per cent, and under conditions of supersaturation up to 169 per cent. Tap-water varied from 54 to 100 per cent, averaging about 85 per cent in surface-water supplies and from 9 to 100 per cent, averaging 61 per cent, in driven-well waters. The amount of free carbon dioxid in rain-water varied from 1.8 to 29 parts per million, with an average of about 7 parts. Streams showed 2 to 19 parts, with an average of 7 parts, and shallow ponds in summer, 3 parts. A reservoir gave 2 to 3 parts at 1 foot, 4 to 11 at 24 to 26 feet, and 16 at 46 feet, while a lake yielded 2 parts at 1 foot, 2.25 at 10 feet, 9 at 25 feet, 11 at 40 feet, and 17 at 50 feet.

Volk (1906 : 13) found the amounts of oxygen in the Elbe River shown in table 12 during the autumn of 1904 and 1905.

TABLE 12.

Date.	Upper Elbe.	Lower Elbe.			
		North side.	Middle.	South side.	Average.
1904	*c.c.*	*c.c.*	*c.c.*	*c.c.*	*c.c.*
Sept. 9	7.03	5.01	5.75	5.75	5.50
Sept. 13	7.51	5.52	5.85	5.82	5.73
Sept. 20	7.48	6.05	6.34	6.41	6.26
Sept. 27	7.56	6.34	6.62	6.52	6.49
Sept. 30	8.53	....	7.60	....	7.60
Oct. 11	8.51	7.68	7.83	7.76	7.76
Averages	*7.77*	.....	.....	.....	*6.56*
1905					
Sept. 5	7.26	5.90	6.20	6.20	6.10
Sept. 12	7.68	5.60	5.94	5.96	5.83
Sept. 19	7.55	5.98	6.16	5.93	6.02
Sept. 26	7.78	6.07	6.65	6.67	6.46
Oct. 3	8.55	6.43	6.62	6.54	6.53
Oct. 10	8.78	6.52	6.84	6.64	6.66
Averages	*7.93*	.....	.....	.....	*6.27*

Hesselmann (1910 : 117) has made an exhaustive study of the oxygen-content of various bog and water habitats in Sweden. The oxygen-content of the water in slowly growing pine forest was 2.49 to 6.08 c.c. per liter, and in spruce moors and swamps, 0.25 to 3.73 c.c., with higher amounts only exceptional. In streams and lakes the amount varied from 5.17 to 7.61 c.c., and in springs and brooks

from 3.36 to 6.84 c.c. In the soil-water of rapidly growing pine forest the range was from 0.88 to 3.30 c.c., the average being approximately 2 c.c. in contrast to 8.2 c.c. at saturation. In pine forest with poor growth, the range was from 0 to 0.88 and the average 0.13 c.c., half of the situations showing no oxygen whatever.

Birge and Juday (1911) have thoroughly investigated the gases in Wisconsin lakes. They have found that the amount of oxygen decreases during the winter in Lake Mendota, the decrease being slight from 1 to 15 meters, but often falling to zero in the bottom water before the ice breaks up in the spring. The layer beneath the ice may reach 130 per cent of saturation on clear days when the algæ receive enough sunlight for photosynthesis. The per cent of saturation due to the evolution of oxygen by algæ was greatest at 4 to 5 meters, where a maximum of 364 per cent was reached. The spring overturn occurs about the time of the disappearance of the ice and results in the equal distribution of the gases throughout the depth of the lake, the oxygen being 8 c.c. per liter. The process of decay reduces the amount of oxygen in the lower water, so that it has entirely disappeared at 18 to 22 meters before the middle of July. During August it may be entirely absent below 10 meters, and is present in small quantities until the fall overturn in October. During the four months, June to September, the amount in the surface 5 feet varied chiefly between 5 and 8 c.c. per liter, with frequent periods of supersaturation for the surface. The amount before the autumnal overturn in October was about 5 c.c. to a depth of 15 meters, while after the overturn about the same amount occurred to 22 meters. From this time the oxygen in the upper water gradually decreased, due to the falling-off of photosynthesis and the rapidity of decay. The amount tends to rise again in November and to approach saturation in December.

The demands of the algæ of Lake Mendota for carbon dioxid are greater than the supply of this gas in the free state. The excess demand is met by the half-bound carbon dioxid, and this results in changing the water from acid to alkaline. The free carbon dioxid is uniform from top to bottom as a result of the autumnal circulation. The amount of carbon dioxid, and hence the acidity, increases during the winter, reaching a maximum of 5 to 9 c.c. near the bottom in March. The spring overturn brings the entire body of water near to the neutral point, after which it becomes increasingly alkaline until the latter part of May, when the water below 18 meters developed free carbon dioxid and became acid. From June to October, the water was alkaline above 8 feet and acid below 15 feet, the 10 and 12 foot depths being acid in midsummer. The overturn in October again made the water uniformly alkaline in reaction.

Chambers (1912) found the oxygen-content of a lagoon to vary from 3.2 c.c. per liter, June 23, to the saturation-point (7.8 c.c.) on

July 20, when the water-bloom appeared. He found 4.6 c.c. of oxygen and 7.7 c.c. of CO_2 in tap-water per liter. The lowest amount of oxygen was 2.32 c.c., when the water was muddy after heavy rains, and the highest amount of CO_2 was 10 c.c., when the lagoon was covered with ice. Richards (1917 : 331) concluded that rain-water is very nearly saturated with oxygen when its temperature as collected is below 15° C., but is less than saturated to as much as 25 per cent when the temperature is above this. The amount of oxygen in summer rain has been shown by Russell and Richards (1919 : 328) to be 95 per cent of saturation and in winter rain 99 per cent. The number of pounds per acre is 26 for the winter from November to February inclusive, and 20.8 for the summer, May to August. It is also estimated that 66.4 pounds of dissolved oxygen per acre is brought down by rain in a year.

Bergmann (1920 : 23) has shown that the oxygen-content of lake and bog water decreases with the amount of vegetation, while that of carbon dioxid correspondingly increases, as seen in table 13.

TABLE 13.

Source.	Sample.	Gas-content per liter.		Source.	Sample.	Gas-content per liter.	
		CO_2.	Oxygen.			CO_2.	Oxygen.
	No.	*c.c.*	*c.c.*		*No.*	*c.c.*	*c.c.*
Hubert Lake (spring water)..	1	1.0	7.6	Mud Lake: Carex-Calamagrostis; Sphagnum abundant...	1	5.8	3.2
Do.....	2	1.4	7.2	Do.....	2	6.0	3.0
Do.....	3	1.2	7.4	Do.....	3	6.0	3.0
Do.....	4	1.2	7.6	Mud Lake, Larix-Picea.....	1	8.4	2.8
Do.....	5	1.2	7.6	Henderson's Bog: Carex.....	1	8.4	4.6
Do.....	6	1.0	7.8	Henderson's Bog: Andromeda, below Sphagnum.....	1	9.8	3.9
				Do.....	2	10.2	3.8

Pearsall (1920 : 171) has determined the changes in the dissolved gases of English lakes during the growing-season in relation to the plant communities. The avergages were expressed in per cent as in table 14.

TABLE 14.

	Apr.	May.	June.	July.	Aug.	Sept.	Dec. and Jan.
Oxygen.....	0.63	0.62	0.56	0.31	0.41	0.46	0.76
CO_2.....	.....	.058	.049	.049	.066	.079	.070

Samples taken above different communities showed no important difference in the carbon-dioxid content (table 15).

TABLE 15.

Soil type.	Plants.	Windermere.		Coniston.	Esthwaite.
		June.	Aug.	Sept.	
5–15 p. ct. humus.	Potamogeton spp..	0.050	0.066	0.076	0.055
15–30 p. ct. humus.	Isœtes or Nitella...	.048	.067	.072	.054

When the CO_2 ranged from 0.055 to 0.067 per cent in the open lake, it varied from 0.066 to 0.084 per cent in a closed bay containing *Castalia, Potamogeton,* and *Carex.*

Bergmann (1921 : 50) has established a relation between the variation in carbon dioxid and oxygen-content of water and the condition of the sky. In one pond with clear water, little vegetation, and a white sandy bottom, the oxygen averaged 6.2 c.c. and the carbon dioxid 0.46 c.c. on clear days, and 5.5 c.c. and 0.17 c.c. on cloudy days. In one filled with vegetation and with a muck bottom, the oxygen averaged 4.7 c.c. and the carbon dioxid, 0.7 c.c. on clear days. In bog ditches the general average was about 4 c.c. of oxygen on clear days and 5.1 of carbon dioxid on clear days, and 2.7 c.c. and 4.5 c.c. respectively on cloudy ones. Where algæ and other vegetation were present, as in the last two cases, there was a much wider variation in the gas-content of the water between day and night, or between clear and cloudy days.

Summary.—Since the amount of oxygen in water is usually determined in cubic centimeters per liter or in percentages of saturation, and the carbon dioxid often in parts per million, it is difficult to establish comparisons with soil-air. This is directly possible only from the researches of Morren and Morren, who found the carbon dioxid in the gas of a vivarium to vary from 1.27 to 24 per cent and the oxygen from 18 to 60 per cent. The maximum amount of CO_2 caused the death of animals and must have had a similar effect upon the plants. Whipple and Parker stated that the amount of oxygen varied from about 9 c.c. in midwinter to about 6 c.c. in midsummer, which approximates saturation at both times. The water of ponds, reservoirs and rivers is usually somewhere near saturation, and often exceeds it. Tap-water is more rarely saturated, the averages being 61 and 85 per cent. Volk found the water of the Elbe to be generally above saturation in September, the amount being greater in the Upper than in the Lower Elbe. Birge and Juday noted 8 c.c. of oxygen in the water of Lake Mendota at the spring overturn, and from 5 to 8 c.c. in the surface 5 feet during June to September, the surface itself often showing supersaturation. Chambers found 3.2 c.c. of oxygen in the water of a lagoon in June, and 7.8 c.c. in July, while Bergman observed an average of 3.4 c.c. in bog water and of 7.4 c.c. in a lake fed by springs. Whipple and Parker obtained an

average of 7 parts of CO_2 per million in rain-water and streams, and of 3 parts in shallow ponds, while a lake ranged from 2 parts at 1 foot to 17 at 50 feet. Birge and Juday found 5 to 9 c.c. per liter near the bottom in the winter, the water above 10 feet being practically without acid during the summer. Bergmann showed that bog-water contained several times as much carbon dioxid as lake-water, the respective averages being 7.8 c.c. and 1.15 c.c.

INFLUENCE OF ALGÆ AND WATER PLANTS ON OXYGEN-CONTENT.

Brizi (1906 : 89) was the first to point out the significance of algæ in the aeration of higher plants. He demonstrated that the algæ from the rice-fields, when placed in cultures of rice containing CO_2 but no oxygen, produced sufficient oxygen to aerate the roots and insure healthy growth. He concluded from this that the algæ of the rice-fields greatly increased the amount of oxygen in the water and were the principal factor in the aeration of the roots. They were regarded as of further advantage in consuming the carbon dioxid that might otherwise accumulate in injurious quantities. Chambers (1912 : 203) found that the photosynthesis of rapidly growing algæ and aquatic plants in a body of water may diminish or deplete the supply of carbon dioxid and increase the oxygen-content beyond saturation. In the absence of free CO_2, the plants may use the half-bound carbon dioxid of the dissolved carbonates, chiefly those of calcium and magnesium. Photosynthesis may be so active as to use up the half-bound carbon dioxid and make the water alkaline, but more carbonates may then be formed as a result of respiration and absorption from the air. Waters rich in calcium carbonates are also rich in vegetation, but bog-waters containing humic acids, and hence poor in carbonates of lime, are poor in vegetation.

Harrison and Aiyer (1913 : 94) were led to the conclusion that the surface film of algæ on rice soils is the chief agency in the aeration of the roots, as indicated by the evolution of oxygen from such soils. In a special study of this film (1914), they determined that green algæ were generally, and diatoms invariably, present, and showed that it decomposed CO_2 in the sunlight, with evolution of oxygen. The film probably also contains bacteria capable of oxidizing methane and hydrogen to carbon dioxid and water, as it carries on these processes actively. The organic film on the surface of the swampy soil of rice-fields utilizes the gases in such a way as to increase the evolution of oxygen and the consequent aeration. The bacterial activity results in the production of more carbon dioxid, and this is used by the algæ with increased production of oxygen. The film permits the maximum oxygen concentration of the water entering the soil. Green manuring increases the soil-gases, supplies more material to the film, and thus augments the evolution of oxygen and consequent aeration.

Bergmann (1920 : 22) has found that *Philotria* decreases the carbon dioxid and increases the oxygen during the day, as shown by tables 16 and 17.

TABLE 16.—*Gas-content per liter of water with and without Philotria.*

No.	Kind of water.	CO_2.	Oxygen.
		c.c.	c.c.
1	Standing tap-water	2.8	5.4
2	Do	2.6	5.6
3	Tap-water, with Philotria, forenoon	2.8	5.4
4	Do	2.6	5.6
5	Tap-water, with Philotria, afternoon	0.6	8.2
6	Do	0.8	7.8

TABLE 17.—*Gas-content per liter of water with Philotria.*

No.	Time.	CO_2.	Oxygen.
		c.c.	c.c.
1	10 a. m	1.1	6.2
2	10 h. 30 m. a. m	0.8	7.0
3	11 a. m	0.5	7.4

Esmarch (1910, 1914) first called attention to the algal flora of soils, and pointed out that algæ occur in the lower layers as well as in the surface-soil. He concluded that cultivated soils are richer in blue-green algæ than uncultivated ones. A later study dealt with the depth and distribution of blue-green algæ in the soils of Schleswig-Holstein. He found that blue-green algæ in cultivated soils are not confined to the surface layers, but that many occur to depths of 10 to 25 cm. and some as deep as 40 to 50 cm., ranging throughout the entire depth. This is due to cultivation, percolation of water, and the burrowing of worms and other small animals. It was also observed that blue-green algæ inclosed in the soil keep green for a time, but gradually become yellowish, and after a further interval the filaments become distorted and disintegrate. This period is 3 to 6 weeks long, or, in one case, as much as 10 weeks long. The author thought that in certain soils the presence of blue-green algæ is an important factor in the fixation of nitrogen by bacteria.

Robbins (1912) found 21 species of algæ in Colorado irrigated soils, all belonging to the blue-green slimes, except *Pleurococcus viridis* and *Navicula* sp. The algæ occurred in all kinds of soil, from sandy loam to heavy adobe, and were probably derived for the most part from the irrigation-water. The most important forms were *Phormidium tenue*, *Nostoc* sp., *Anabœna* sp., *Nodularia harveyana*, and *Stigonema* sp. The organic matter furnished by the algæ was

regarded as an important source of energy for the nitrogen-fixing organisms, especially *Azotobacter*, and this serves to explain the accumulation of unusually large amounts of nitrates in certain Colorado soils. This has been confirmed by Hutchinson (1918), who has shown that the activity of *Azotobacter* is appreciably increased by the addition of plant residues to the soil.

Moore and Karrer (1919 : 281) have studied the subterranean algal flora of several soils from Missouri, Massachusetts, and California, and have concluded that this flora is independent of the nature of the soil and locality. The variety of algæ was not large, though comparable with that on the surface. *Protoderma viride* was the most common species by far, while the blue-green algæ supplied the majority of the other forms. The former occurred to the greatest depth, 1 meter, and in every soil, indicating its special ability to live underground. It is concluded that the algal flora rises from the surface forms, but that its persistence at considerable depths indicates that the algæ actually grow in the soil, since it is assumed that surface waters are unable to carry them so deeply in such compact soils as clay.

Bristol (1920 : 35) has found 64 species of algæ in soils from widely separated localities. Of these, 20 are diatoms, 24 blue-green algæ, and 20 yellow-green algæ. The most common species are *Hantzchia amphioxys, Trochiscia aspera, Chlorococcum humicola, Bumillera exilis,* and *Ulothrix subtilis variabilis,* with much moss protonema. These were found to be able to withstand complete desiccation for 4 to 26 weeks. The author suggests that the presence of algæ in the soil must affect the soil gases.

Summary.—It has been shown by a number of workers that algæ may bring about the supersaturation of lakes and streams as a consequence of photosynthesis. This frequently amounts to 200 to 300 per cent of saturation and has been found to reach 550 per cent. At the same time, algæ and other water-plants prevent the accumulation of large amounts of CO_2 as a result of the same process. Brizi, and Harrison and Aiyer, have shown the importance of the algal film of rice-fields for the aeration of the roots, and Bergmann has demonstrated the value of *Philotria* and *Spirogyra* in furnishing a supply of oxygen for submerged roots. Esmarch, Robbins, Moore and Karrer, and Bristol have studied the algal flora of soils, and the first two have concluded that the algæ are an important source of organic material for nitrogen-fixing bacteria. Bristol suggests that the presence of algæ may affect the soil-gases. It seems certain that this must be the case in soils sufficiently moist to permit their growth, and that they then increase the aeration and prevent the harmful action of carbon dioxid in the same manner as in rice-fields.

AIR-CONTENT OF PLANTS.

Aimé (1841 : 537) analyzed the bubbles on the surface of marine algæ, such as *Ulva*, as well as those in the interior, with the results shown in table 18.

TABLE 18.

Bubbles.	Before sunrise.	Before sunset.
Internal:	*p. ct.*	*p. ct.*
O.....	17	36
N.....	83	64
External:		
O.....	21	55
N.....	79	45

Unger (1854) determined that the floating leaves of *Pistia texensis* contained the maximum amount of air, 71.3 per cent by volume, while the fleshy leaves of *Begonia hydrocotylifolia* showed the least, 3.5 per cent.

Faivre and Dupré (1866) investigated the composition of the internal air in the organs of the mulberry under various conditions, with the results shown in table 19. They found that the carbon dioxid diminished and the oxygen increased as activity was reduced, and that the amount of oxygen was less and of CO_2 greater in roots than in branches during the growing-season.

TABLE 19.

Date.	Organ.	O.	CO_2.
1865		*p. ct.*	*p. ct.*
Mar.	Leafless branches.....	21.0	....
May 15	Leafy branches.....	13.33	3.33
June 15	Do.	2.5	15.7
July 2	2-year shoots.....	10.21	6.3
July 7	Roots.....	1.9	14.6
Aug. 17	Shoots of the year.....	10.7	9.0
Oct. 15	Branches, activity reduced.	13.96	3.19
Oct. 16	Roots.....	7.5	3.76
Nov. 17	Shoots of the year.....	13.1	3.8
Nov. 24	Roots, after leaf-fall.....	16.6	1.6
1866			
Jan. 31	Branches, inactive.....	20.9	0.01

Heintz (1873 : 358) analyzed the composition of air inside the sugar-beet with the results given in table 20.

TABLE 20.

	1	2	3	4	5
CO_2.....	30.52	35.10	11.49	41.02	78.90
O.....	0.14	0.56	1.53	2.10	0.06
N.....	69.34	64.34	86.98	56.88	21.04

Barthelemy (1874 : 175) gave a summary of the analyses of internal air in connection with his own determinations (table 21).

TABLE 21.

	O.	CO_2.	N.
	p. ct.	*p. ct.*	*p. ct.*
Aimé (marine algæ)	17	.....	83
Saussure (branch of apple)	9	5	86
Boussingault (oleander)	6.64	5.34	88
Martins and Moitessier:			
Jussiæa	15.8	.....	84.92
Aldrovandia	15.5	.....	84.5
Pontederia crassipes	14.1	.....	85.9
Dutrochet (Nuphar luteum):			
Rootstock	16	.....	84
Root	8	.....	82
Leaves	18	.....	82
Lechartier (Nuphar luteum, petiole)	12	.....	88
Barthelemy (Nelumbo)	10	3	87
Do.	14	trace	76
Do.	15	2	83
Do.	22	0	78

Wille (1889) found the air of *Fucus* bladders in water to contain 35 to 37 per cent of oxygen, 20.7 to 20.8 per cent in those dried in air 10 hours, and but 2.7 per cent in those lying in the dark for 12 hours. Carbon dioxid was completely absent in all cases.

Devaux (1889 : 115), studying the gas-exchange of aquatic plants, made the analyses of the gas in and about the plant and of the air shown in table 22.

TABLE 22.

	CO_2.	O.	N.
	p. ct.	*p. ct.*	*p. ct.*
Air from interior of stem of Elodea	2.14	18.86	79.40
Air at surface of leaves and stems	0.69	23.08	76.23
Air collected by wax funnel	0.30	23.59	76.11
Air contained in the water	21.10	31.04	66.87
Composition of surrounding air	0.04	18.66	81.30

The author concluded that the air dissolved naturally in water possesses essentially the same pressure as in the atmosphere. As to the internal air of the plants, if the water is normally aerated, the air of the air-passages or spaces is nearly pure. The air arrives at each cell with nearly the same pressure as that which it possesses in the surrounding water and in the air-passages. There is some air simply dissolved in the substance of the cell itself, and this possesses the same pressure as at the exterior.

In measuring the oxygen-content of a tubercle (1890 : 257), Devaux concluded that the oxygen never wholly disappears in the

midst of massive tissue. In conditions especially unfavorable to gas exchange, the amount of oxygen falls very low, to about 0.25 per cent. In all the cases observed, however, its total disappearance never occurred. The diffusion of free air is vastly more rapid than that of dissolved air, a fact which permits very perfect aeration of porous tissues, but very imperfect in culture fluids. The central cavity of a fruit of *Cucurbita maxima* contained air with a composition of 2.52 per cent CO_2, 18.29 per cent oxygen, and 79.19 per cent N. When air was forced into the fruit under water, numerous larger and smaller bubbles appeared over the surface, coming from what are essentially lenticels. In the fruits of cucurbits that lack lenticels the air enters through the stomata.

Aubert (1892 : 203) found the composition given in table 23 for the internal air of several species of succulent plants.

TABLE 23.

	CO_2.	O.	N.
	p. ct.	*p. ct.*	*p. ct.*
Crassula arborescens (sunny)	1.50	26.45	72.05
Crassula arborescens (cloudy)	0.22	22.78	77.00
Sedum dendroideum (sunny)	0.85	18.35	80.80
Phyllocactus grandiflorus (sunny)	0.41	25.33	74.26
Opuntia tomentosa (sunny)	0.67	24.02	75.31
Opuntia dejecta (sunny)	0.47	25.63	73.90

Magness (1920 : 308) has analyzed the gas in the intercellular spaces of apples, potatoes, and carrots at different storage temperatures, with the results included in table 24.

TABLE 24.

Products stored.	Temperature of storage.	No. of determinations.	CO_2.	O.
	° *C.*		*p. ct.*	*p. ct.*
Apples	2	5	6.7	14.2
Do.	6	30	8.4	12.9
Do.	11	27	12.2	10.7
Do.	20	31	17.2	5.5
Do.	30	29	21.4	3.2
Potatoes	11	8	19.6	10.9
Do.	22	8	34.4	5.7
Carrots	11	2	12.2	13.1
Do.	22	2	28.6	5.2

The removal of the peel from the ends of apples resulted in a marked reduction in the amount of CO_2 and a similar increase of oxygen, due to the greater ease of escape and entrance. The range of variation in the amounts of these two gases at 20 C. was 12.5

to 25.7 per cent for carbon dioxid and 1 to 9.5 per cent for oxygen. The chief factors determining the amounts are the rate of respiration, the permeability of the peel or skin, and the difference in the pressure of the two gases within and without the tissue.

Summary.—The composition of the internal air of plants depends primarily upon the presence or absence of photosynthesis. Stems, leaves, and other chlorophyllous parts contain air with much oxygen and little carbon dioxid, while roots, tubers, ripe fruits, etc., show much carbon dioxid and relatively small amounts of oxygen. Aimé found 17 per cent of oxygen in the internal gas-bubbles of *Ulva* and 21 per cent in the external before sunrise, and these increased during the day to 36 and 55 per cent respectively. No carbon dioxid was present. According to Wille, the bladders of *Fucus* contained 35 to 37 per cent of oxygen in the water, 20 per cent when exposed to the air 10 hours, and but 2.7 per cent after 12 hours in darkness. Saussure obtained 9 per cent of oxygen and 5 per cent of CO_2 from an apple twig, Boussingault, 6.64 per cent of oxygen and 5.34 per cent of carbon dioxid from oleander, and Barthelemy, 10 to 22 per cent of oxygen and 0 to 3 per cent of CO_2 from *Nelumbo*. Dutrochet found 18 per cent of oxygen in the leaves of *Nuphar*, Lechartier, 12 per cent in the petiole, and Martins and Moitessier, 14 to 15.8 per cent in other water-plants. The air of the interior of the stem of *Elodea* was shown by Devaux to contain 8.86 per cent of oxygen and 2.14 per cent of CO_2; the air at the surface of leaves and stems, 23 and 0.69 per cent respectively; that of the water, 31 and 21 per cent; and the surrounding air, 18.66 and 0.04 per cent. The air in the center of a squash was composed of 18.29 per cent oxygen, 2.52 per cent carbon dioxid, and 79.19 per cent nitrogen (cf. Pfeffer, 1900, 1 : 205).

According to Aubert, the air of succulent plants yielded 18.35 to 26.45 per cent of oxygen and 0.47 to 1.50 per cent of carbon dioxid in the sun. *Crassula arborescens* contained 7 times as much CO_2 in the sun as under a cloudy sky. Dutrochet found but 8 per cent of oxygen in the root of *Nuphar*, while Magness has recently shown that apples, potatoes, and carrots stored at 11° C. and above, regularly contain much more CO_2 than oxygen. At 20° to 22° apples averaged 17.2 per cent of carbon dioxid and 5.5 per cent of oxygen; potatoes, 34.4 and 5.7 per cent; and carrots, 28.6 and 5.2 per cent.

ANAEROBIC RESPIRATION.

The significance of reduced air-content and of the respiratory products arising from it in saturated soils is so great as to warrant a comprehensive account of anaerobic respiration. This lacks completeness chiefly with reference to the theories concerning the nature of intramolecular respiration and fermentation, and to the nature and rôle of the enzymes concerned. In organizing the large

mass of results, the primary divisions are based upon the functions and organs studied. These are respiration itself, photosynthesis, transpiration, germination, growth, protoplasmic movement, and irritability. The fungi are discussed separately, in consequence of their more or less peculiar behavior. The effects of the various agents employed in producing anaerobic conditions are summarized in the discussion at the end of each section and the significance of anaerobic respiration in explaining the problems discussed is dealt with in the succeeding chapters.

RESPIRATION.

Early researches.—As already indicated, Huygens and Papin (1674) were the first to show that plants could not grow in vacua, while shortly afterward Ray (1686) and Homberg (1699) found that under similar conditions seeds failed to germinate or did so only with difficulty. Ingenhousz (1779) observed that plants died in air unfavorable to animal life as well as in pure carbon dioxid. Humboldt (1794) and Rollo (1798) thought that seeds germinated more readily in oxygen than in air, and Lefebure (1801) observed that germination was greatly retarded by low oxygen-content. The classic experiments were those of Huber and Senebier (1801) and Saussure (1804) upon germination and growth, which are considered in detail under these sections. Rollo (1798 : 37) was the first to observe the phenomenon of anaerobic respiration in noting that barley grains gave off a considerable quantity of carbon dioxid for several days when oxygen was absent. Dumont (1819) and Döbereiner (1822) found that fruits, especially apples and pears, developed a demonstrable amount of alcohol after they had been subjected to an atmosphere of CO_2 for a certain time. Bérard (1821) demonstrated that fruit kept in an atmosphere of carbon dioxid exhibited the phenomena of fermentation. When oxygen was withheld, green fruits were unable to ripen, but the ripening process was resumed when they were again placed in air, providing the anaerobic conditions were not too prolonged. Cahours (1864 : 635) likewise found that oranges respired in the absence of air, evolving carbon dioxid in an atmosphere of nitrogen.

Later researches.—The proper understanding of the nature of anaerobic respiration was first made possible by Pasteur's researches in fermentation (1861, 1872, 1876). He stated that the yeast of beer behaved altogether like an ordinary plant and that it was probable that certain lower plants could live without air in the presence of sugar, producing under these conditions a fermentation similar to that of yeast. He later experimented with wine grapes kept in an atmosphere of CO_2 and came finally to the view that the respiration was analogous to that of yeast. He concluded that the formation of alcohol was due to the fact that the cells of the fruit continue to

live under the new conditions in a manner similar to that of ferments. He found that when fruit is placed in an atmosphere of CO_2, respiration proceeds in consequence of the decomposition of sugar. The cells are in the condition of ferments which live without free oxygen, as in the case of cells of *Mycoderma vini* when submerged. In fact, as soon as the fruit is placed in CO_2, both carbon dioxid and alcohol are produced in small amounts, while the fruits remain firm and entirely sound in appearance.

Lechartier and Bellamy (1869; 1872; 1874) determined that CO_2 and alcohol were formed when fruits were kept in a closed receptacle without oxygen, though it was impossible to find an alcoholic ferment in them. Further study of the respiration of fruits showed that cherries, gooseberries, figs, and lemons, as well as beets and potatoes, and the leaves of cherry, gooseberry, etc., behaved as did pears and apples in the earlier experiments. They concluded that life does not stop in the cells of a fruit or leaf as soon as detached from the plant. Activity continues under the exclusion of the air through the consumption of sugar and with the production of alcohol and CO_2. The moment at which the production of CO_2 ceases is at the final death of the cell. As a consequence, fruits, seeds, and leaves can remain inert indefinitely if micro-organisms do not develop in them.

Dehérain and Moissan (1874 : 356) found that leaves placed in an atmosphere deprived of oxygen continued to evolve CO_2 for several hours, the evolution apparently ceasing only when all the cells were dead. The resistance to death in the absence of oxygen varied greatly from one species to another. They also showed that CO_2 produced a slowing down of respiration, while Borodin (1875) obtained similar results in contrast to the behavior in an atmosphere of hydrogen. Dehérain and Vesque (1876 : 327) studied the absorption of oxygen and the emission of carbon dioxid by roots, in extension of the work of Saussure. In addition to confirming the normal behavior of roots in air, they placed them in pure oxygen, and also in air deprived of oxygen. The former gave no bad effects in the case of *Veronica*. Plants of the latter lived for 7 days in an atmosphere of nitrogen, and those of ivy for 15 days, but finally the leaves fell and the plants died. Plants of ivy placed in an atmosphere of pure carbon dioxid died speedily, the leaves drying up and the vegetative point falling away. They also showed (1877 : 959) that a feeble excretion of carbon dioxid occurs when oxygen is absorbed by the root. Plants did not seem to suffer by the substitution of oxygen for the air in the soil about the roots, but the emission of CO_2 was somewhat greater. When small amounts of CO_2 were added to the soil-air or to oxygen, the plant did not appear to suffer, but it died if kept in pure CO_2. It also died when the roots were kept in an atmosphere of nitrogen, but the action was much less rapid.

De Luca (1878 : 301) stated that fruits, flowers, and leaves in an atmosphere of carbon dioxid or hydrogen, in a vacuum, or in restricted air, gave off CO_2, nitrogen, and, in some cases, hydrogen, with the formation of alcohol and acetic acid, as a consequence of the action of a ferment.

Godlewski (1882 : 521) found that a reduced oxygen-pressure exercised a definite effect upon respiration. The absorption of oxygen was greatest in the case of the plants in air, and, as the oxygen-content of the air was reduced, absorption decreased. The reduction of the respiration intensity was due solely to reduced oxygen-pressure, as the plants regained their earlier intensity when the apparatus was opened, and the reduced absorption of oxygen was not observed in the case of plants in pure oxygen. The intensity of respiration was found to be different with the seeds of different species. Under similar conditions, flaxseed respired more than those of hemp and radish, and these again more than alfalfa. The respiration energy was much less in the case of germinating starchy seeds than with oily ones. Moreover, the starchy seeds differed among themselves strongly in this respect; 1 gram of germinating wheat grains absorbed in the same time and under similar conditions considerably more oxygen than 1 gram of peas. Swollen peas in the first stage of germination in pure oxygen absorbed considerably more of this gas in the same time than in the air. Moreover, the production of CO_2 in such seeds was hastened by the action of pure oxygen, though in less degree. When the swelling of seeds took place with the air excluded, as under water, intramolecular respiration began. This did not cease immediately when the seeds were placed again in the air, but was gradually replaced by normal respiration. As soon as oily seeds showed rootlets, the volume of CO_2 evolved lagged more and more behind that of the oxygen absorbed. In the germination of starchy seeds, the volume of CO_2 evolved was nearly the same as that of the oxygen absorbed in all stages. The changes of the pressure of the oxygen affected the respiration energy of different plant parts in a very different manner. When the respiration dealt with fats, the intensity depended more upon the oxygen-pressure than where it took place at the expense of carbohydrates.

In a study of intramolecular respiration, Wortmann (1882 : 520) concluded that while oxygen takes a part in the formation of new chemical compounds through intramolecular activity, its presence has a critical effect upon the continuance of molecular change. Even when plants possess the ability to exist for a time when deprived of oxygen, this must be regarded not as a normal but as a pathological condition, since both photosynthesis and growth are inhibited.

Johannsen (1885 : 716) confirmed Bert's general results that the physiological results of compressed air were to be ascribed to the increased partial pressure of oxygen. Higher oxygen-pressures up

to 5 atmospheres at first increased the evolution of CO_2 for the different seedlings investigated and in varying degree for the different species. With longer action, the CO_2 decreased gradually until death ensued, and the more rapidly, the greater the pressure. After two to four hours' exposure to oxygen of a pressure of 2 to 5 atmospheres, the plants showed a considerably greater evolution of CO_2 than before the exposure when they were again returned to the original conditions.

Pfeffer (1885 : 645) found that the amount of CO_2 evolved when seedlings were placed in hydrogen was regularly less than in the air. Respiration in the latter was often several times greater, with the exception of *Vicia faba*, where the amounts were about equal. The respiration of sun-roses in ordinary air, in mixtures of equal parts of air and hydrogen, and of 1 part of air and 4 parts of hydrogen was essentially the same. Intramolecular respiration, as shown by a considerable decrease of the CO_2 produced, occurred in a mixture of 19 parts of hydrogen and 1 of air.

Diakonow (1886 : 411) demonstrated that the excretion of carbon dioxid by cotyledons of the bean was 50 per cent greater in the absence of oxygen than in its presence. He reached the conclusion that fermentation begins immediately upon the withdrawal of oxygen and disappears again just as soon as the cells resume their full capacity for respiration. As a consequence, there can be no respiration, and hence no life, without the presence of oxygen or the action of fermentation as the one means of meeting the energy needs of the cell.

Palladin (1886 : 44) determined that rootlets of *Vicia faba* consumed 4.6 per cent of dry material in 20 hours of normal respiration, and 11 per cent during the same period in air free from oxygen. Since they used more than twice as much dry substance in the latter in spite of the gradual decrease of activity, anaerobic respiration must be regarded as true fermentation.

Clausen (1890 : 893) investigated the behavior of dead protoplasm with respect to the evolution of CO_2 and also the decomposition of albumen in the living protoplasm when oxygen is absent. With reference to the former, he found that living plants evolved 27 to 28 mg. of CO_2 in an hour, while the same plants when killed gave from 1.5 to 2.1 mg., which was little more than within the limits of error. He concluded in agreement with Detmer, Johannsen, and Pfeffer, and contrary to Reinke's opinion, that dead plants do not evolve CO_2. The albumen of the protoplasm of plant-cells when this is in contact with oxygen, as is well known, breaks down into acid amides and amino-acids, and his experiments showed that a similar breaking-down occurred in the absence of oxygen.

Stich (1891 : 1) concluded that respiration is independent of the oxygen-content of the environment within fairly wide limits. With

oxygen-contents of 20.8, 8, 6, 4, 2, and 0 per cent, the point at which a decrease of the CO_2 production appeared was different for different plants. On an average, however, a striking reduction of the carbon dioxid produced did not take place between 4 and 2 per cent. At 2 per cent, flowers of *Anemone japonica*, fruits of *Prunus domestica*, and seedlings of *Helianthus*, *Triticum*, and *Vicia* respired normal amounts of CO_2, while flowers of *Stenactis annua*, *Cacalia verbascifolia*, fruits of *Hippophaëa*, and seedlings of *Brassica napus* and *Cucurbita melanosperma* showed a marked decrease of CO_2. With a number of fruits the amount of CO_2 was not influenced by the oxygen-content, since these produced as much CO_2 in hydrogen as in the air. The respiration quotient was not influenced by a content of 8 per cent and an exposure period of 3 to 24 hours, but at 3 to 4 per cent of oxygen the quotient was changed, with a resulting increase of CO_2.

Ziegenbein (1893 : 564) found that seedlings of *Lupinus* exhibit a breaking down of the albumen in the absence of oxygen, as well as in its presence. Diakonow (1894) repeated his earlier experiments upon the dependence of molds upon the presence of oxygen, using *Penicillium glaucum*, *Aspergillus niger*, and *Mucor stolonifer*. With the first two, activity was found to be wholly dependent upon oxygen, the excretion of carbon dioxid ceasing instantly in pure hydrogen. *Penicillium*, moreover, died quickly in the absence of oxygen, even in solutions containing sugar or glycerin. *Mucor*, on the contrary, showed no injury when grown in a sugar solution, and continued to produce CO_2 in a stream of pure hydrogen.

Palladin (1894), in applying Diakonow's discovery to flowering plants, found that, while etiolated leaves of *Vicia faba* and *Lupinus luteus*, free from carbohydrates, evolved but small amounts of CO_2 and quickly died in the absence of oxygen, those that had absorbed sugar produced carbon dioxid much more rapidly and retained their activity longer.

Godlewski and Polzeniusz (1897) showed that peas in oxygen-free media were able to use 40 per cent of their original weight in respiration. In spite of the accumulation of alcohol in the culture, intramolecular respiration continued for 6 weeks, the intensity being maintained for 3 weeks at the level of that of normal respiration. They also showed that the seeds retained their power of germination for 2 weeks under anaerobic conditions.

Buchner (1897 : 117) first showed that yeast contains a ferment, zymase, capable of transforming glucose into alcohol and CO_2. Devaux (1899) found that the deep-seated tissues of woody stems above a certain diameter are lacking in free oxygen, and hence undergo fermentation with the formation of carbon dioxid and alcohol. This condition exists at ordinary temperatures, but is augmented by raising the temperature. Direct analyses of the gas of

such tissues showed oxygen to be present in only one-thirty-fifth of the volume.

Recent researches.—Gerber (1903 : 269) found that increased oxygen increased the respiratory quotient and hastened the ripening of unripe bananas, but decreased the respiratory quotient of ripe bananas.

Smirnoff (1903 : 32) showed that wounding produced no increase in intramolecular respiration. The latter at first decreased in hydrogen, but nearly or quite regained its original intensity in about 40 hours, beginning to fall off again on the fifth day. If, however, the wounded bulbs were placed in air instead of hydrogen between experiments, there was an increase in the energy of intramolecular respiration nearly proportional to that of the normal respiration.

Stoklasa, Jelinek, and Vitek (1903 : 493) reached the conclusion that the anaerobic respiration of the sugar-beet is essentially identical with alcoholic fermentation by yeast. In both cases, CO_2 and alcohol are the chief products, while by-products appear in insignificant quantity. The same quantitative relations between CO_2 and alcohol occur as in alcoholic fermentation by yeast. They regard it as fully demonstrated that the anaerobic respiration of sugar-beet under the complete exclusion of microbes is an alcoholic fermentation, and that its products, alcohol and CO_2, are true excretions. The presence of enzymes similar to those of invertase and zymase shows that the anaerobic respiration of the sugar-beet is extraordinarily like that of the yeast-cell.

Godlewski (1904) observed that lupine seeds in pure water without oxygen developed only a very weak intramolecular respiration for 6 to 8 weeks. This could be greatly strengthened by adding the proper sugar. In the latter case the intramolecular respiration depended upon alcoholic fermentation. In solutions of both fruit-sugar and cane-sugar the seeds may germinate partially without access of oxygen and the radicles reach a length of 3 to 6 mm., when they slowly die. He concluded that the decomposition of albumen can occur in the absence of oxygen, but that the synthetic formation of asparagin as the beginning of albumen regeneration was impossible with the higher plants.

Gola (1905) studied the seeds of *Trapa natans* and the rhizomes of *Nuphar luteum* and *Nymphæa alba* during the period of rest as well as of germination and found alcohol present in the storage tissues. He thought this to be due to the unfavorable conditions for aeration in swamps, which result in anaerobic respiration.

Palladin and Kostytschew (1906) made further studies of anaerobic respiration in relation to alcoholic fermentation, with the following results: A considerable amount of alcohol is formed in the anaerobic respiration of living seeds and seedlings of *Lupinus*, and the

anaerobic respiration of these is, therefore, really identical with alcoholic fermentation. The anaerobic respiration of frozen seeds and seedlings produced no alcohol, and that of a frozen stem-tip of *Vicia faba* no amount worth noting, and hence bears no relation to alcoholic fermentation. A considerable amount of alcohol was produced in the anaerobic respiration of living and frozen seeds of peas and castor beans and of wheat germs. The anaerobic respiration of these objects is, therefore, chiefly alcoholic fermentation, since the zymase was not destroyed. With living peas an accumulation of alcohol was observed only in the absence of oxygen. Frozen peas, on the contrary, accumulated considerable amounts of alcohol with complete access of oxygen. This is explained by the fact that the oxidation processes in plant-cells are weakened in consequence of killing. With both normal and anaerobic respiration of living and frozen plants, acetone and various acids were formed under certain conditions.

Stoklasa, Ernest and Chocensky (1906 : 302) concluded that in most cases anaerobic respiration is an enzymatic process identical with alcoholic fermentation. This is true of the anaerobic respiration of the frozen organs of seed-plants, as well as of the leaf and root of the sugar-beet, and the tubers of the potato. Under anaerobic conditions they isolated noticeable quantities of lactic acid from sugar-beets.

Palladin and Kostytschew (1907 : 51) studied the anaerobic respiration of etiolated plant parts and concluded that seed-plants can produce alcohol only in the presence of carbohydrates. In the absence of these, anaerobic respiration leads to the production of CO_2 without the formation of alcohol.

Kostytschew (1908 : 537) assumed that the intermediate products of alcoholic fermentation are oxidized under the access of oxygen and that alcohol in consequence is to be regarded as a by-product of respiration which is not produced under normal conditions. He further concluded (1913 : 129) that in the majority of cases the anaerobic respiration of seed-plants is not identical with zymase fermentation, since in most cases other reactions occur along with the latter.

Stoklasa and Ernest (1908) subjected roots of *Hordeum vulgare* and *Zea mays* to an atmosphere consisting of 94 per cent nitrogen and 6 per cent oxygen, and roots of buckwheat to 94 per cent hydrogen and 6 per cent oxygen, and found that they secreted acetic and formic acids. They concluded that these acids are formed only when there is a lack of oxygen for the normal oxidation processes of the root. With the proper access of oxygen, acetic and formic acids are further changed in the living cell, and are finally broken up into carbon dioxid and hydrogen, the latter probably being largely oxidized to water. The roots of buckwheat, rye, oats, and corn all showed formic acid in the absence of oxygen, while rye yielded acetic

acid as well. They cited the work of Aso (1906) which showed that acetic and formic acids, even in greatly diluted solutions, exerted an unfavorable influence upon lower as well as higher plants. Moreover, the salts of both of these acids in similar concentrations were poisonous to plant organs. Aso explained this poisonous effect of the salts of formic and acetic acids as probably due to hydrolytic dissociation in the living cell of these salts into acids and bases, by which the base was absorbed by the proteids, while the acid was released and acted unfavorably upon the living protoplasm. Acid aldehyde and acetone were always found alongside of acetic and formic acid, all of which have been shown by Aso to be poisonous.

Babcock (1912 : 150) confirmed the results of earlier investigators upon the behavior of apples and pears under anaerobic conditions, and noted that there was practically no difference in the final results when hydrogen, nitrogen, carbon dioxid, or the residual gas of respiration was employed, or the fruits immersed in cotton-seed oil. Succulent tissues of all kinds behaved in similar fashion in the absence of oxygen, but in young tissues the production of acids was found to be more rapid and the life of the cells short.

Hill (1913) reached the following conclusions respecting the anaerobic respiration of fruits: The anaerobic production of CO_2 by ripe cherries, blackberries, and grapes is as rapid as the aerobic production for a considerable length of time. Ripe fruits that spoil quickly, such as cherries, have a higher respiratory rate than those that do not spoil so quickly, such as grapes. This is due possibly to a higher enzyme-content. Fruit tissues that respire as actively anaerobically as aerobically seem to be those that have finished their growth and are ripe. Growing tissues, such as green peaches and germinating wheat, respire more than twice as rapidly aerobically as anaerobically. The activity of the protoplasm would seem to be connected with the more direct use of oxygen in the production of CO_2. If growing tissues, such as green peaches, are placed in an oxygen-free gas for a few days and then brought back into air, the rate of production of CO_2 does not entirely return to the normal. This would indicate a permanent injury to the protoplasm or to some of the enzymes, due to insufficient oxygen. Ripe apples lose their color, texture, and flavor, and take on the qualities of half-baked apples, by being kept for a sufficient length of time in oxygen-free gases (N, H). This emphasizes the need of good aeration for apples. The softening of peaches seems to be decreased greatly by CO_2 and to a considerable extent by hydrogen and nitrogen. Peaches become brownish and acquire a very bad flavor when oxygen is withheld from them. "Ice-scald" seems to be an injury due to insufficient oxygen and to an accumulation of CO_2 within the paper wrappers in which peaches are so often shipped. With good ventilation in conjunction with good refrigera-

tion, such injury may be greatly reduced. This applies to fruits in storage as well as to those in transit.

Noyes (1914 : 792) gradually saturated the soil in which corn and tomato plants were growing with washed CO_2. The lower parts of the plants were first affected and in a week the leaves drooped, turned brownish, and withered. The plants were practically browned at the end of 2 weeks' treatment, the tomato showing the most marked effect. After the treatment, oxygen was given access to the plants. The tomato plant soon died, but the corn plant revived and was growing normally at the end of a week.

Hasselbring (1918 : 284) found that sweet potatoes are killed under an oxygen-pressure of 5 atmospheres, and that starch hydrolysis is greatly depressed or prevented in the killed tissues. The hydrolysis of starch and the formation of cane-sugar take place in the absence of oxygen as in the air or in an atmosphere of oxygen, and the presence of oxygen is thus not always necessary to the formation of cane-sugar. The material consumed and the output of carbon dioxid is greater in the sweet potato during anaerobic than during normal respiration.

Summary.—The general effect of the reduction or absence of oxygen upon respiration is to decrease its intensity, as shown by Godlewski, Wilson, Johannsen, Palladin, Stich, Hill, and others. On the contrary, Diakonow found the intensity to be greater in the cotyledons of the bean, but this is probably due to their nature as specialized storage-organs. Even in *Penicillium* and *Aspergillus* he found that the production of carbon dioxid ceased immediately upon the withdrawal of oxygen. The reduction in oxygen-content required to affect respiration differs more or less with the species, and this serves in some measure to explain the discordant results. Saussure determined that the oxygen could be reduced one-half without weakening respiration, while Wilson found that the latter was but slightly affected in a mixture containing 20 per cent of air, though distinctly decreased in one with 5 per cent. Stich stated that in general a striking reduction in the amount of carbon dioxid did not occur between 4 and 2 per cent of oxygen.

Saussure and Grischow concluded that the rate of respiration was somewhat increased in pure oxygen, but Bert observed a decrease in the amount of CO_2 evolved after several days' exposure. While Böhm and Rischawi found that plants were more or less indifferent to high oxygen-content, Godlewski obtained a strikingly greater production of carbon dioxid for the first day, after which it fell to a minimum. Johannsen likewise noted that the respiration intensity under an air-pressure of 10 to 15 atmospheres, corresponding to a pure-oxygen pressure of 2 to 5 atmospheres, was more or less increased for a few hours, after which it gradually decreased to the death point, and the more rapidly under the greater pressure.

Pfeffer showed that the evolution of carbon dioxid in the air was several times greater than in hydrogen, and Pasteur, Borodin, Dehérain and Moissan, Vesque, and others that it is greatly reduced in an atmosphere of CO_2 itself, continued exposure resulting in the death of the plant. Pfeffer (1900) has stated that most land-plants die eventually in an atmosphere containing from 4 to 20 per cent of carbon dioxid.

As would be expected, respiration under anaerobic conditions differs with the species, much as does normal respiration. This fact may be readily gained from practically all experiments dealing with two or more species, and it has been studied especially by several investigators. Dehérain and Moissan stated that in the absence of oxygen the resistance of leaves to death varied greatly from species to species and they confirmed this for roots as well.

Godlewski found that the energy of respiration was much smaller in starchy than in oily seeds during germination under reduced oxygen-pressure, and starchy seeds also differed much among themselves. The increased evolution of carbon dioxid under oxygen-pressure up to 5 atmospheres varied with the species in the investigations of Johannsen, while Pfeffer observed a wide range in the amount evolved by seedlings in hydrogen from *Vicia faba*, which gave nearly equal amounts in air and in hydrogen, to those in which the normal respiration was several times greater. At 2 per cent of oxygen, Stich showed that certain flowers, fruits, and seedlings respired normal amounts of CO_2, while others showed a marked decrease. Hill found that ripe fruits which spoil quickly, such as cherries, respired more intensely under anaerobic conditions than those that keep better, such as grapes.

Finally, Stoklasa and Ernest have determined that the roots of rye secrete both formic and acetic acid in the absence of oxygen, but those of buckwheat, oats, and corn acetic acid alone.

Carbon dioxid and alcohol are the regular products of anaerobic respiration, and the latter is consequently regarded by most investigators as essentially identical with alcoholic fermentation when carbohydrates are present. Under certain conditions it approaches other types of fermentation, and acetic, formic, and lactic acids have frequently been noted as excretions from the roots and other parts of flowering plants. Among the fermentation products arising from anaerobic respiration are amyl, butyl, and ethyl alcohols, acetic, butyric, citric, formic, lactic, oxalic, propionic, and valerianic acids, acid aldehyde, and acetone, while the decomposition products are ammonia, fatty amido-acids, leucin, skatol, tyrosin, sulphureted hydrogen, mercaptan, etc. Hydrogen is a frequent product, and methane, carbon monoxid, and nitrogen rarer ones (Pfeffer, 1900 : 533).

PHOTOSYNTHESIS.

The first studies of the effect of pure carbon dioxid upon photosynthesis were made by Grischow (1819), who found that this process was greatly reduced but not wholly prevented in the sunlight and with the gas at the ordinary air-pressure. Boussingault (1868 : 269) confirmed Grischow's results, and concluded that the reduction was due to the excessive partial pressure of the carbon dioxid, rather than to the absence of oxygen, as the latter was constantly produced in the sunlight. When the carbon dioxid was mixed with other gases, or its pressure reduced, its depressing effect was less marked. He also found (1865 : 605) that oleander leaves lost the ability to free oxygen from a mixture of CO_2 and ordinary air after 48 hours' retention in carbon dioxid, nitrogen, or marsh-gas in the dark at a temperature of 22° to 23° C. In the case of a single leaf, which had been kept for 48 hours in hydrogen in the dark, 2.6 c.c. of carbon dioxid were broken down after 5 hours of insolation. In the case of many plants, while photosynthesis was slight in pure carbon dioxid, it was marked in mixtures containing 30 and even 40 per cent.

Pfeffer (1871) observed that both 8 and 16 per cent of carbon dioxid in the air were without noticeable effect upon the evolution of oxygen from the leaves of *Prunus laurocerasus*.

Böhm (1873 : 230) found that leaves of laurel plants, after remaining several hours in an atmosphere without oxygen, perished or completely lost the capacity to break down carbon dioxid. However, they continued to live, obtaining the necessary energy for their functions through intramolecular respiration. He also studied the influence of CO_2 upon the greening and growth of seedlings, and found that this gas exerted a strikingly injurious effect. In a mixture of 2 per cent its unfavorable effect upon chlorophyll formation was noticeable. In air whose oxygen-content corresponded to that of ordinary air, but contained 50 per cent of CO_2, not only did no growth occur, but the plants themselves died after a short time. In view of the fact that plants visibly sickened in an atmosphere which contained only a few per cent of CO_2, it was concluded that the present plant world would perish, at least in part, in an atmosphere not much richer in CO_2 than the existing one. From this it results either that the compostion of the atmosphere on earth has been the same from the beginning, which seems a necessary consequence of its being limitless, or, what was regarded as less probable, that there were plants in earlier periods which could endure a greater amount of CO_2 without damage.

Godlewski (1873 : 243) endeavored to determine the optimum amount of CO_2 for photosynthesis, and found it to lie between 5 and 10 per cent for *Typha*, *Glyceria* and *Nerium*, while greater amounts

were more or less injurious. His experiments lasted but a short time and gave no light upon the effect of long-continued exposure.

Schützenberger and Quinquand (1873) found that the maximum photosynthesis in *Elodea* was at 5 to 10 per cent of CO_2 dissolved in water; it was reduced by 20 to 30 per cent, and ceased in saturated CO_2.

Warburg (1886 : 122) found that the differences in photosynthesis for *Nerium* were not very significant at 5 to 25 per cent, while in *Bryophyllum*, photosynthesis was slight at 12 per cent and minimum at 20 per cent. *Hoplophytum grande* showed a marked reduction at 10 to 15 per cent.

Pfeffer (1887) likewise observed that photosynthesis was suppressed in the absence of oxygen. Correns (1892) confirmed the conclusion of Wiesner that oxygen is necessary for the greening of etiolated plants. This occurred at 4 per cent for *Helianthus*, 5 per cent for *Sinapis*, and 8 per cent for *Lepidium*.

Brown and Escombe (1902 : 397) determined that a leaf responds to increased carbon dioxid in the air around it within certain limits. With 2 to 4 times as much CO_2 in the air, the activity of photosynthesis was increased, but the gain in dry weight was less than in ordinary air. The effect upon the plant was shown by shorter, thicker internodes, a more bushy habit due to the development of axillary buds, smaller leaves, and the almost complete suppression of flowers. They concluded that the sudden increase of CO_2 in the atmosphere to 2 to 3 times the present amount would destroy nearly all flowering plants.

Crocker and Davis (1914) determined that no chlorophyll developed in seedlings of *Alisma* during a month's exposure to an air-pressure below 5 mm.

Summary.—All results are in accord as to the harmful effect of carbon dioxid upon photosynthesis and the production of chlorophyll. The latter function appears the more susceptible, as Böhm observed that injury was produced at 2 per cent, but an extensive study of this relation in a wide range of plants is much to be desired. Böhm also determined that several hours' exposure to an atmosphere devoid of oxygen was sufficient to destroy the power of photosynthesis, and Boussingault obtained similar results from the use of carbon dioxid, nitrogen, or marsh-gas for 48 hours. Grischow found that pure carbon dioxid greatly reduced but did not wholly prevent photosynthesis in the sunlight, and Boussingault stated that, while it was slight in the pure gas, it was marked at 30 and even 40 per cent. These percentages are much higher than those obtained by other investigators, and it seems probable that they were due to the dilution of the gas by the oxygen freed in the sunlight.

The varying response of different species is shown by the fact that Pfeffer discerned no effect from 8 and 16 per cent of carbon

dioxid in the case of *Prunus*, and Warburg but little in *Nerium* at 5 to 25 per cent, while Schützenberger and Quinquand found 5 to 10 per cent the optimum for *Elodea*, and Warburg observed that photosynthesis was markedly reduced in *Hoplophytum* at 10 to 15 per cent, and was but slight in *Bryophyllum* at 12 per cent. Although Brown and Escombe showed that photosynthetic activity was increased with 2 to 4 times the normal amount of CO_2 in the air, the gain in dry weight was less, the stems and leaves were reduced, and the flowers were almost completely suppressed.

The significance of the injurious effect of carbon dioxid on photosynthesis upon the question of the greater amount of this gas in the atmosphere during earlier geological periods was first pointed out by Böhm, who regarded it as probable that the composition of the atmosphere has remained the same since the beginning of plant life on the land. This view receives further support from the conclusion of Brown and Escombe that a sudden increase in the carbon dioxid of the atmosphere to 2 to 4 times the present amount would destroy most flowering plants.

TRANSPIRATION.

Saussure (1804) was the first to observe that pea plants wilted in an atmosphere of carbon dioxid, as well as in mixtures containing three-fourths and two-thirds of it when this gas was led into the nutrient solution in which they were growing, and Wolff (1870 : 134) confirmed this in the case of barley and beans. Barthelemy (1873) also found that transpiration was reduced by the action of dry carbon dioxid. In a study of the effect of very dilute acids upon transpiration, Burgerstein (1876 : 202) determined the influence of carbon dioxid. In three preliminary experiments with corn seedlings in which the amount of CO_2 was not known, the transpiration generally was much greater for the plants in distilled water. In the series proper, the solutions contained respectively 0.08 and 0.04 per cent of carbon dioxid. The plants in the stronger solution transpired slightly more than those in distilled water, and those in the weaker slightly less in the case of corn. All the other plants studied, peas, beans, pumpkin, broad beans, *Celtis*, *Fagus*, *Tilia*, *Cratægus*, and *Salisburia*, regularly showed considerably greater water-loss in the CO_2 solution.

In a study of the absorption of free nitrogen by legumes, Kossowitsch (1892 : 702) found that an atmosphere of 80 per cent CO_2 and 20 per cent oxygen worked injury to the root-system. When the roots of peas had been in such an atmosphere only 2 days, the plants began to wither and they grew no further. As soon as the CO_2 was removed from the inclosed soil and the latter aerated, the peas regained their normal turgescence. He also found that when the soil was penetrated by a stream of mixed oxygen and hydrogen, the plants were not injured.

Kosaroff (1897 : 604) in a study of the effect of temperature and gases upon absorption, found that a lack of oxygen and the accumulation of CO_2 exerted an unfavorable influence upon the functions of the plant. He was especially concerned to determine how far the absence of oxygen was injurious and what part the presence of undesirable gases played. He found that pure CO_2 diminished both absorption and transpiration. Plants whose roots were placed for some time in an atmosphere rich in CO_2 soon lost their turgor, became limp, and commonly died after further action. The injurious effect of CO_2 is its particular property, but it also emphasizes the withdrawal of oxygen, and its influence upon absorption is, therefore, of a double nature. On the contrary, the depressing effect of hydrogen operates only through the withdrawal of oxygen, and is much weaker than that of CO_2. Both gases also influence absorption unfavorably when the root is cut off. Pure CO_2 affects the transpiration of plants whose roots have been killed by scalding. The author concluded that not only is the activity of the root influenced by this gas, but it also enters the roots and probably exerts an influence on the width of the stomatal opening, thus further reducing the transpiration. In the case of seedlings, leafy and leafless shoots and twigs (1900 : 138), carbon dioxid strongly depressed absorption and hence transpiration, regardless of the part used. It worked injury wherever it came into contact with living cells. This was both a direct consequence of the action of CO_2 and an indirect result of the exclusion of oxygen. The wilting of plants with continued access of CO_2 was ascribed to the depression of the transpiration stream.

Livingston and Free (1917 : 183) found that absorption by the roots of *Coleus blumei* and *Heliotropium peruvianum* ceased within 24 hours after replacing the soil-air with nitrogen. Within 1 to 6 days this was followed by loss of turgor in shoot and leaves, and finally by wilting and death. In *Nerium oleander,* the disturbance of water-relations in the shoot was indicated by the yellowing and loss of leaves. *Coleus* recovered slowly with renewed access of oxygen, while *Heliotropium* failed to do so after wilting became extensive. The roots of the injured plants were found to be dead and partially disintegrated. New roots were formed from the base of the stem in *Coleus* on the readmission of oxygen. The injury due to the lack of oxygen was found to be greatest with the plants possessing the larger root-systems. The roots of *Salix* were found to function normally in the absence of oxygen.

Bergmann (1920 : 14) observed that geranium plants wilted in a few days after the roots were subjected to carbon dioxid, the wilting evidently beginning before all the oxygen was replaced. After wilting, the leaves turned yellow and fell off to the end of the experiment. *Impatiens balsamina,* under similar treatement, was slightly

wilted on the second day and badly on the third. It was then given access to the air, but failed to recover.

Summary.—The depressing action of high percentages of carbon dioxid upon absorption and transpiration has been shown in all the investigations concerned. A similar result has been obtained by Livingston and Free by the use of nitrogen. In practically all cases the pure gas was employed, and hence it is uncertain at what points injury begins. It appears probable that with many species a disturbance of the water-relations occurs at 5 or 10 per cent, or even lower, and that in water-logged soils and in bogs carbon dioxid may operate by reducing absorption as well as respiration and photosynthesis. Kossowitsch was the first to show that CO_2 exerted a specific effect, regardless of the presence of oxygen, and this was confirmed by Kosaroff, who emphasized the fact that the injury wrought was due to the poisonous property of carbon dioxid as well as to the withdrawal of oxygen. The results of Burgerstein with exceedingly dilute solutions do not contravene the rule, but serve to show that carbonic acid in minute quantities behaves like many other acids that stimulate absorption and transpiration.

GERMINATION.

Early researches.—The earliest studies of germination in a vacuum were made by Boyle (1660), Ray (1686), Homberg (1699), Boerhaave (1724), and Musschenbroek (1729). Their results were all in agreement to the effect that seeds germinated poorly or not at all in vacua, though they did readily upon renewed access of air. Humboldt (1794) and Rollo (1798) concluded that seeds germinated more readily in oxygen than in ordinary air, while Huber and Senebier (1801) found that germination was poorer in oxygen obtained chemically. Rollo also determined that seeds would not grow in hydrogen or nitrogen. Ingenhousz (1786) germinated cress seeds in oxygen, but was unable to do so in hydrogen.

Lefebure (1801 : 94) investigated the germination of radish seeds in a number of gases. When placed in nitrogen, they failed to germinate during a sojourn of 12 days, while in oxygen nearly all had germinated by the end of 3 days. Repeated experiments gave the same results in oxygen. No germination occurred in carbon dioxid or in hydrogen in a period of 12 days. When oxygen was mixed with nitrogen, carbon dioxid, hydrogen, or a combination of nitrogen and CO_2 in the proportion of 1 to 8 or 1 to 16 parts, the seeds germinated as readily as in ordinary air. When the amount of oxygen was reduced to one thirty-second, however, some failed to grow and the others did so more slowly than in the air.

Huber and Senebier (1801) were the pioneers in an exhaustive study of the relation of air and other gases to germination. Inter-

estingly, Huber performed all the experiments, while Senebier furnished the suggestions and wrote the text. It was seen that seeds would not germinate in air whose oxygen had been exhausted by bees. Peas, beans, lentils, and wheat germinated under water, while many other seeds would not. When the water was deep, the radicle appeared at first, but fermentation ensued and the plants died. Peas began to decompose in 24 hours in water that had been boiled. It is perhaps significant that peas, beans, and spinach alone germinated readily under water, and that only a few seeds of other species succeeded in pushing forth the radicle. Carbon dioxid alone was given off at first, but hydrogen appeared with the beginning of fermentation.

Seeds of lettuce placed in oxygen derived from green plant parts were seen to germinate more rapidly than in ordinary air, as well as to develop their seedlings more rapidly, but the latter were sometimes injured by the gas. In oxygen obtained from manganese the seeds germinated less rapidly. The favorable effect of oxygen drawn from green parts was confirmed by the seeds of wheat, beans, kidney beans, and spinach. Seeds germinated better in a mixture of 3 parts of nitrogen or hydrogen and 1 of oxygen than in 3 of the latter with 1 of either of the other two. In 1 to 4 parts of oxygen and hydrogen germination was very good, in 1 to 5 it was slow and the seedlings perished sooner, while in 1 to 7 but five seeds had germinated at the end of 3 days and the radicles died immediately. While Lefebure found that the seeds of turnip germinated in nitrogen containing one thirty-second part of oxygen, Huber was able to germinate lettuce only when the oxygen reached a sixth. Carbon dioxid, when mixed with varying amounts of oxygen, prevented germination in all cases, while some germination took place with all but the minimum amount of oxygen in hydrogen.

Lettuce seeds refused to germinate in pure nitrogen, regardless of its manner of derivation, but most of them germinated readily when placed again in the air. Peas, however, germinated readily enough in pure nitrogen. With varying mixtures of nitrogen and oxygen, germination did not occur until the one containing 4 times the initial amount of oxygen. The greater number of seeds did not germinate in pure hydrogen, though they grew readily enough in mixtures of it with ordinary air or oxygen. With the latter, growth failed only with the mixture containing the smallest amount of oxygen. While peas germinated in hydrogen, lettuce required 7 days instead of 22 hours, and wheat, barley, and oats did not grow at all. All seeds exposed to pure carbon dioxid refused to germinate, and many of them were unable to do so when brought into ordinary air afterward.

Saussure (1804) found that no germination took place in pure hydrogen, but green plants persisted in it practically as well as in

nitrogen. In the best vacuum obtainable some seeds, such as peas, germinated to the point of the appearance of the radicle, but no further. Seeds were unable to germinate in pure carbon dioxid, and even a small amount retarded germination, both in sun and shade.

John (1819 : 282) found that swollen peas showed no germination after 4 weeks in carbon dioxid in the light, but that they began to germinate in 3 days in a mixture of one-third carbon dioxid and two-thirds ordinary air. No further growth occurred in the course of 2 weeks, even with access of air, as decomposition had set in. He concluded that CO_2 killed the embryo as well as the young seedling, and that germination was possible only when the amount of air exceeded that of carbon dioxid.

Döbereiner (1822 : 212) germinated barley in one-half normal atmospheric pressure and under a pressure of 2 atmospheres. The germination proceeded at an equal rate under both bell-glasses, but the seedlings grew faster in the compressed air than in the rarefied.

Later researches.—Böhm (1873) observed that wet seeds in pure oxygen at the ordinary pressure did not go beyond the first stage of germination, but that they thrived just as well as in atmospheric air when the oxygen was mixed with four-fifths of its volume of hydrogen or reduced to a pressure of 150 mm. The development of beans was at a minimum in the case of seeds in pure oxygen. It was not the lack of nitrogen but too high a pressure of oxygen that produced this, since the germination of the bean proceeded normally in pure oxygen when the pressure was reduced to one-fifth of the normal. The same amount of oxygen was absorbed when the germination took place in pure oxygen or in the air. He obtained the same results with peas, lentils, and corn, while seeds of sunflower, cress, and flax were much less influenced by high oxygen-pressure. The development of the seedlings was somewhat weaker in pure oxygen than in ordinary air. The results also indicated that oily seeds can germinate under a much higher oxygen-pressure than starchy ones. He later found (1874 : 180) that germination was delayed by 5 per cent CO_2, while in germinating cress the formation of chlorophyll was delayed by 2 per cent CO_2, prevented by 20 per cent, and entirely suppressed by 2 days' stay in the gas.

Dehérain and Landrin (1874 : 382) determined that seeds germinate in pure oxygen, but less rapidly than in atmospheric air. Whenever oxidation in the seed had begun, it continued even in an atmosphere deprived of oxygen, and the volume of CO_2 produced was greater than the original volume of oxygen. Hydrogen appeared ordinarily only in an atmosphere in which the oxygen had completely disappeared, and carbon dioxid was shown to be more injurious to germination than nitrogen or hydrogen.

Bert (1876 : 1493) observed that an increase of the air-pressure to 4 or 5 atmospheres, or of the oxygen-content to 60 per cent, was either without any influence upon germination or merely hastened it. But when the oxygen rose to 80 or 90 per cent, or the air was compressed beyond 5 atmospheres, the harmful effect of the increased oxygen-pressure was quickly evident. Germination was delayed and the growth of the plants was weaker than under normal conditions, the greater the pressure the weaker being the plant. The germination of starchy seeds suffered much more from the increased pressure than that of oily seeds, and the latter could stand a much higher pressure without damage. As for respiration itself, a much smaller volume of oxygen was absorbed at a pressure of 11 atmospheres than under normal conditions. Under reduced air-pressure, germination took place more slowly the lower the pressure. It ceased between 4 and 10 cm. without the seeds dying.

Giglioli (1879 : 477; 1895 : 544) found that seeds of wheat, *Cynara, Vicia,* and *Phaseolus* kept their power to germinate longer in CO_2 than in ordinary air when they were dry, but that they were killed very quickly in it when wet. Wet seeds kept in oxygen and in carbon monoxide failed to germinate. Seeds of alfalfa that had been kept in hydrogen for 16 years gave a germination of 56 per cent, while those in carbon monoxid gave 84 per cent.

Bernard (1883 : 200) noted that seeds of cress were not able to germinate in a mixture of air with one-sixth volume of CO_2. When exposed afterward to air, germination took place in normal fashion.

Van Tieghem and Bonnier (1882 : 25) found that peas left in open air for 2 years gave 90 per cent of germination, while those in restricted air gave but 45 per cent, and in carbon dioxid, none germinated. For beans, the respective percentages were 98, 2, and 0. Castor-beans gave similar results, while wheat and flax showed little difference in open and in closed air, but all agreed in failing to germinate in CO_2.

Linossier (1889 : 820) concluded that amounts of CO_2 up to 19 per cent delayed germination, and above this the number of germinating seeds decreased with increasing content, but that germination was entirely suppressed only at higher percentages. Lettuce seeds still germinated at 36 per cent, though cress seeds would not. Carbon dioxid was considered to be a poison to which seeds were variously susceptible.

Lukas (1886 : 298) found that a varying air-pressure from 22 to 72 mm. was sufficient for the germination of seeds of *Avena sativa, Triticum vulgare, Panicum miliaceum,* and *Cucurbita pepo,* but not sufficient for the further development of the young seedling, or for the germination of *Brassica rapa, Lactuca sativa,* etc. Atmospheric air under a pressure of 70 to 168 mm. was sufficient for the growth

of the young plants of practically all of these, although in some it resulted in a slower rate of growth than in normal air.

Dehérain (1892 : 8) proved that lack of oxygen prevented germination in water by placing seeds in a tube traversed by a current of aerated water. The seeds at the entrance germinated perfectly, while the ones at the other end did not grow and finally decayed, owing to the consumption of the oxygen by the former.

Ewart (1894 : 215) demonstrated that prolonged immersion in unchanged water greatly reduced germination. While the percentage varied from 44 for barley to 95 for beans after 5 days, germination failed after 10 days in the case of beans, 14 days for peas, and 3 weeks for wheat, barley, and flax. This was confirmed in later experiments (1896 : 185), which also showed that the same seeds retained their viability several weeks longer in sterile water free from oxygen.

Lopriore (1895) found that pollen-grains form protuberances in pure CO_2, but these soon burst; others are unable to germinate and still others burst in it. Pollen-tubes formed in the air and then placed in pure CO_2 burst for the most part. A content of 1 to 10 per cent carbon dioxid markedly promoted the growth of the pollen-tube, but not its turgor-pressure. The latter increased steadily when tubes were placed in air after 20 minutes in CO_2.

Jodin (1897 : 442) observed that peas submerged in mercury for more than 4 years showed 80 per cent of normal germination, but when submerged nearly 6 years longer, gave but 22 per cent of normal germination and 22 per cent of abnormal, while 56 failed to germinate. Seeds of pea and cress gave no indication of germinating in 58 per cent CO_2. When returned to ordinary air, all the cress seeds germinated within 2 days, but none of the peas, showing that the latter were killed by the gas. It was found that 7 per cent CO_2 did not hinder or greatly modify the germination of peas, while at 13 per cent the radicle appeared only with difficulty and its growth stopped at 2 to 3 mm. At 50 per cent the power of germination was quickly lost, although respiration continued for some time. Peas in stagnant or sterilized water showed only the first stage of germination, while they germinated normally in running water.

Recent researches.—Mazé (1900 : 350) observed that the seeds of most land-plants will not germinate under water, and that immersion soon leads to the loss of the power to germinate. Germination of immersed seeds was produced by thorough aeration of the water or by means of hydrogen peroxid.

Schaible (1900 : 93) studied the germination of seeds of *Phaseolus, Lepidium, Satureia, Vicia* and *Hortensia* under reduced air-pressure of 3 different grades and confirmed the results of Bert to the effect that it was slower and less complete than in the air.

Kolkwitz (1901 : 285) has shown that the respiration of barley with a moisture content of 10 to 11 per cent is very weak, averaging less than 1 mg. CO_2 per kilogram per day. It rises rapidly with increasing moisture and reaches 2,000 mg. per day for each kilogram at 33 per cent, while if the temperature and oxygen-content of the air are raised, it reaches astounding amounts. When seeds are cut into halves, the part containing the embryo respires three times as much as the one with endosperm alone. If the grains are ground in a coffee-mill, respiration increases 50 per cent, due either to wounding or to easier access of oxygen. Respiration does not stop if the grains are ground to meal.

Duval (1904 : 79) kept the seeds of cabbage and onion in a vacuum for 182 days and found that they germinated 75 and 73 per cent respectively, in comparison with 81 and 74 per cent for controls. During the period no evolution of gases occurred.

Takahashi (1905 : 439) found that peas could not germinate in the absence of air, although intramolecular respiration was carried on for a number of weeks. Rice grains were able to germinate in plain water and in the absence of air. This was explained by the fact that rice grows naturally in places where germination must occur in the presence of very little oxygen. In the experiment, however, growth seemed to stop when the young plumule reached the length of 3 cm.

Crocker (1906 : 273) has shown that delayed germination in the cocklebur is due to the exclusion of oxygen by the seed-coats. While the coats of both upper and lower seeds reduce the amount of oxygen, reduction is greatest for the upper. With the coats removed, lower seeds absorb 1.6 to 1.7 times as much oxygen as with them intact, while the upper take up 2 to 2.4 times as much. Seeds of *Xanthium canadense* soaked for 12 to 18 hours and then kept at 21° to 23° C. for 6 days showed complete germination in pure oxygen and none in air. He further demonstrated (1907 : 378) that delayed germination of the seeds of water-plants is due to the exclusion of water by the seed-coats. Oxygen does not seem to be concerned, as increased pressures do not effect germination with the coats intact, and little oxygen is needed, moreover. Seeds with intact coats showed no germination after 10 days, while those with the coats broken gave the following percentages at the end of 1 and 10 days respectively: *Alisma plantago*, 86, 98; *Eichhornia*, 96, 98; *Polygonum amphibium*, 81, 85; *Potamogeton natans*, 42, 51; *P. pectinatus*, 47, 53; *Sagittaria variabilis*, 92, 92; *Typha latifolia*, 85, 89.

Shull (1911 : 475) has found a marked difference in the demand for oxygen by the embryos of the upper and lower seeds of *Xanthium*. In seeds without coats, the minimal oxygen pressure at 21° C. is about 9.5 mm. for the lower seeds and 12 mm. for the upper. A rise of 10° in temperature lowers these minima to 3 mm. and 7 mm.

respectively. The seeds of cocklebur can not germinate without relatively large amounts of oxygen, being opposite in this respect to seeds of *Alisma* and rice. They do not support the view that the seeds of higher plants can grow in the entire absence of oxygen.

Babcock (1912 : 99) determined that corn containing 6 to 8 per cent of water kept for a year in CO_2 germinated more slowly than that kept in the air, while corn with 30 per cent of water kept in carbon dioxid for 8 to 12 months entirely failed to germinate. Kernels of corn immersed for one or more days in water boiled free from air did not germinate until oxygen was supplied.

Becker (1912 : 21) demonstrated that seeds of *Dimorphotheca* germinated more readily in oxygen than in air, especially those from the ray-flowers. Exposure to oxygen for 30 hours was found to promote germination in the air. When the seed-coats were removed, germination was favored by 10 hours' exposure to oxygen, but delayed by exposure for 13 hours. The normal seeds of *Calendula* germinated much more readily in oxygen, while those of *Atriplex* were injured by increased oxygen-pressure.

Atwood (1914 : 386) concluded that the delay in the germination of the seeds of *Avena fatua* was due to the oxygen supply as a limiting factor. This is indicated by the results obtained by breaking or searing the seed-coats or the removal of the embryo, by the amount of germination occurring in different concentrations of oxygen, and by measuring the rate of oxygen absorption in seared and intact seeds. The increased permeability of the seed-coat to oxygen was regarded as a factor in the process of after-ripening.

Pack (1921 : 41) has shown that the catalase activity of seeds stored 45 days at 25° C. rises steadily with the increase of oxygen from 30 to 100 per cent and that the activity at 80 per cent equals that in air.

Kidd (1914) has found that CO_2 in relatively small quantities in the atmosphere inhibits germination, the actual percentage varying with temperature and oxygen supply. Inhibition was produced by 2 to 4 per cent at 3° C., while 25 to 30 per cent was required at 20° C. With 5 per cent oxygen, 9 to 12 per cent CO_2 brought about inhibition, while 20 to 25 per cent was required with 20 per cent oxygen. In all seeds tested, except *Brassica alba*, germination followed normally when CO_2 was removed.

Kidd and West (1917 : 457) have shown that the effect of CO_2 in inhibiting germination in *Brassica alba* is followed by a secondary effect of prolonged dormancy after the gas is removed. If the conditions during the primary period of CO_2 inhibition are injurious, due to lack of oxygen or excess of carbon dioxid, secondary dormancy does not occur. A high percentage of the latter can only be produced by a mixture of 20 to 30 per cent CO_2 and not less than 15 per cent oxygen. Secondary dormancy in the seeds of *Brassica alba* is not

due to increased mechanical pressure of the seed-coats or to their decreased permeability to gases, but to a stable condition of the embryo slowly established during the period of inhibition by carbon dioxid. This is contrary to the results of Crocker on *Xanthium* (1916), Shull on *Xanthium* (1911), and Rose on *Datura* and *Martynia* (1915), all of whom ascribed the effect to the low permeability of the testa to oxygen, and a similar conclusion is indicated by Atwood for *Avena fatua* (1914).

Summary.—Since germination is essentially a matter of respiration and growth, it shows much the same response to anaerobic conditions. The earliest investigators found that it was poor or altogether absent in a vacuum, and similar results were obtained when the oxygen was removed by other means. Rollo and Lefebure observed that seeds would not germinate in pure nitrogen or hydrogen, while Huber and Senebier stated that peas would do so, but lettuce would not. They were unable to germinate most seeds in hydrogen, in agreement with the results of Ingenhousz and Saussure, who obtained no germination in it. The experiments of Huber and Senebier, Saussure, Dehérain, Ewart, and Mazé have shown that seeds germinate but poorly or not at all under water, especially when this is deep and quiet. Rice germinates more readily under water than the seeds of mesophytes, but the growth of the seedling seems to be inhibited sooner or later. Reduction in the amount of oxygen or its pressure beyond a certain point regularly delays or decreases germination. Lefebure found that it took place normally in one-eighth or one-sixteenth oxygen, but failed for the most part in one thirty-second. Huber, however, was able to germinate lettuce seed only when the oxygen reached a sixth. Döbereiner germinated barley at half the normal air-pressure, and Bert, Lukas, and Schaible showed that considerable reductions in pressure retarded germination more or less in proportion.

Contrary to the opinion of Humboldt and Rollo that seeds germinate more readily in pure oxygen, most investigators have found that the latter delays germination. Böhm noted that wet seeds in pure oxygen stopped their development in the first stage, and Dehérain and Landrin observed that germination was less rapid than in atmospheric air, while Huber and Senebier had long before shown that it was better in a mixture of 3 parts of hydrogen or nitrogen and 1 of oxygen than when the amounts were reversed. In Bert's experiments, an air-pressure of 4 to 5 atmospheres or an oxygen content of 60 per cent affected germination little or not at all, but above this it was more or less delayed.

Small amounts of carbon dioxid usually delay germination and higher percentages inhibit it. Saussure stated that a small amount retarded germination, and Böhm found that 5 per cent was sufficient

to produce delay. Bernard obtained no germination with cress in 16 per cent CO_2, while Linossier concluded that it was merely delayed at percentages up to 19, and completely suppressed only at much higher ones. Jodin observed that 7 per cent affected the germination of peas but little, but that it occurred only incompletely at 13 per cent. The explanation of this wide variation apparently has been furnished in part by Kidd, who finds that germination is inhibited by 2 to 4 per cent of carbon dioxid at 3° C., while 25 to 30 per cent was required to bring it about at 20° C. Even more significant differences in response are occasioned by the use of different species. Huber and Senebier early showed that peas, beans, lentils, and wheat would germinate under water, though the seeds of most species would not, and Böhm found similar differences in germination in pure oxygen. Bert observed that the germination of starchy seeds suffered more from high oxygen-pressure than that of oily ones, and Jodin noted that peas were more susceptible to CO_2 than cress seeds.

GROWTH.

Early researches.—While Scheele (1777) thought that plants could not develop well in pure oxygen, and Ingenhousz (1786) found that seedlings thrived better in it, Saussure (1804) was the first to make a study of growth under anaerobic conditions. In pure oxygen, pea plants in the shade were found to gain only half the weight that they did in ordinary air, while in the light the gain was practically the same in both cases. Plants without green parts were unable to grow in pure nitrogen, nor were seeds able to germinate in it, but decomposed quickly, as shown by seeds of pea, cress, and *Polygonum amphibium*. Buds of *Populus nigra* and *Salix alba*, which were ready to open, were unable to develop further in nitrogen, even in the sunshine, but decomposed at the end of 15 days. Buds of roses, lilies, and violets about to open were unable to develop in pure nitrogen. *Opuntia* in pure nitrogen died in the shade in 6 days; in sunshine, it survived for 3 months, but with great difficulty. Some pea plants were able to resist the effect of nitrogen for 4 to 5 days. Such marsh-plants as *Lythrum salicaria*, *Epilobium hirsutum*, *molle*, and *montanum*, and *Polygonum persicaria* grew as well in nitrogen in weak light as they did in ordinary air. Plants of pea, bean, and kidney-bean died in 3 days in a vacuum, either in sun or shade, while fleshy plants, such as *Opuntia*, lived for a month in the sun. The marsh-plants mentioned above grew as readily in vacua as in ordinary air, but this was considered to be due to the large amount of oxygen contained in their tissues. It was concluded that plants can survive or grow in vacua only by the aid of the oxygen evolved from their green parts. Both seeds and roots died in a vacuum, woody plants could not open their leaf-buds in it, and flower-buds showed the same effect. With an eighth of CO_2 the average growth was 371 mg. and

with a twelfth 583 mg. In the shade, the smallest addition of carbon dioxid proved injurious. The plants died in 6 days in a fourth, and in 10 days in a twelfth. A superabundance of CO_2 was more injurious to a plant in nitrogen than in ordinary air, for, while a twelfth of carbon dioxid in ordinary air was not injurious to marsh-plants, they died in a few days with such an amount in nitrogen.

John (1819) showed that plants which were brought into an atmosphere of 33 to 50 per cent of CO_2 or more developed poorly. Davy (1821 : 205) also observed that plants showed but poor growth in air that contained one-third to one-half of its volume of CO_2. Birner and Lucanus (1866 : 160) endeavored to determine the effect of CO_2 in a nutrient solution on growth. Carbon dioxid was led into the solution every 2 or 3 days, but an unfavorable effect was observed in neither of the two plants. On the contrary, they developed excellently and were much stronger than those not acted upon by CO_2. The conclusion was reached that the action of free CO_2 is favorable to the production of dry weight, though it was thought that this was due to the actual use of the gas by the leaves, either by absorption through the roots or by diffusion through the air.

Later researches.—Bert (1873, 1878) made a comprehensive study of growth in reduced air-pressure and in reduced oxygen-content, as well as under increased air-pressure and increased oxygen-content. He was able to show that air-pressure as such had no influence upon growth, but that the latter was influenced only by the partial pressure of the oxygen. Studies with the germination of corn, barley, and cress showed that the process took longer in a pressure of 50 to 25 cm. than with a normal air-pressure, and that germination finally ceased at a pressure of 8 to 7 cm. In the case of *Mimosa pudica* it was found that the leaves fell and the plant quickly perished under a pressure of 25 cm. Algæ were found to cease growth at a similar pressure.

Böhm (1873 : 141) found that the development of seedlings in pure oxygen was usually restricted to the first stage in germination, and concluded that the injury was not due to the lack of nitrogen, but to the density of the oxygen itself. In general, the growth of plants from a supply of reserve material was as a rule reduced to a minimum in pure oxygen of ordinary density. However, growth took place with the same intensity as in atmospheric air when the oxygen was so rarefied by the air-pump or the admixture of hydrogen that it possessed a pressure equal to or even smaller than the partial pressure of atmospheric oxygen.

Rischawi (1876) repeated the experiments of Böhm, but he did not find the development of bean, pea, and corn seedlings so near the minimum as Böhm, although it was weaker than in ordinary air. The most important result was that the rootlets of the plants in

oxygen were 4 to 5 times shorter than in the case of those in the air. He found further that the respiration intensity remained the same, whether the seedlings were in oxygen or in air.

Wortmann (1879) carried out an extensive series of experiments with seeds, seedlings, and shoots in order to determine the nature and significance of intramolecular respiration. His results indicated that the latter was unable to furnish energy for growth processes, though he concluded that life could persist for several days after the withdrawal of oxygen. He was unable to find the slightest growth in the absence of oxygen.

Detmer (1881) repeated and extended the studies of Wortmann, employing N_2O, H, and CO_2 with seeds and seedlings of *Pisum* and *Triticum*. He found neither germination of seeds nor growth of seedlings to occur, while both heliotropism and geotropism were suppressed, as well as the formation of chlorophyll. The plants suffered markedly and quickly perished.

Wilson (1882 : 93) repeated the experiments of Wortmann with seedlings of *Vicia faba* and confirmed the observation that, for a short period, CO_2 was excreted just the same, whether oxygen was available or not. When the experiment continued in the absence of oxygen there was a gradual decrease in the production of CO_2, because the plant became injured. With other seedlings, as with flowers and other plant parts, just as soon as the access of oxygen was cut off a direct decrease took place in the evolution of CO_2. This decrease was usually one-half to three-fourths of the normal respiration. In an atmosphere consisting of one-fifth air and four-fifths hydrogen, the seedlings of *Helianthus annuus* showed no noticeable decrease in CO_2, but a mixture of one-twentieth air and nineteen-twentieths hydrogen resulted in a marked decrease.

Wieler (1883 : 223) determined that plants require atmospheric oxygen for growth, with the exception of certain fungi of fermentation and decomposition. Growth ceased at once in the absence of oxygen, but the amount necessary for growth was very small, ranging from a fraction of a cubic centimeter for *Helianthus annuus* and *Vicia faba* to 1 to 7 c.c. for *Brassica* and *Ricinus*. With decreasing pressure, growth was at first increased, then reached an optimum, decreased with further rarefication, and finally ceased. The growth optimum was determined for *Helianthus annuus* and *Vicia faba*. For the former it was about 3 per cent and for the latter 5 to 6 per cent of oxygen in relation to the contents of the bell-glass. A slowing down of growth in comparison with growth in normal air occurred at 0.14 to 0.5 per cent for *Helianthus*, 1.45 per cent for *Vicia* and *Lupinus luteus*, and 5 to 6 per cent for *Cucurbita pepo*. In pure oxygen, *Helianthus* and *Vicia* grew more rapidly than under normal pressure. In an oxygen-content corresponding to an air-pressure of 2 to 2.5 atmospheres, growth seemed to be slowed down in comparison with

that in normal air. In the case of *Helianthus*, no growth occurred under entire exclusion of oxygen, and it ceased as soon as the oxygen was excluded. Growth began again when the plants were placed in atmospheric air, if they had not been without oxygen for too long a time. Continued exposure to an oxygen-free medium worked serious injury in most cases to the plant. *Helianthus* suffered exposure for 24 hours without damage, and grew vigorously when brought again into atmospheric air. *Vicia faba*, on the contrary, suffered so after 22 hours that the plants blackened when placed in atmospheric air, and *Cucurbita* died on the second day after being returned to it.

Möller (1884) repeated Detmer's experiments with N_2O, using seedlings of *Vicia faba*, and found that no growth occurred, though the seedlings suffered no damage in the 48-hour exposure.

Palladin (1886) exposed seedlings of *Vicia faba* for 20 hours to hydrogen and was entirely unable to find any growth, in contrast to the behavior in air.

Jentys (1888 : 452) stated that, with a single exception, in no case was a complete stoppage of growth observed under greater oxygen-pressure, but in all there was more or less marked reduction. Under approximately equal periods of exposure, the reduction of the growth of the stem parts was the greater the higher the pressure. He pointed out that these results were in opposition to those of Bert, but explained this by the fact that Bert's experiments lasted 4 days in contrast to 4 hours. Raising the partial pressure of oxygen to one atmosphere was decidedly favorable to the growth of seedlings of *Raphanus*, *Sinapis*, and *Brassica*, but without any influence upon the growth of *Vicia*, *Helianthus*, and *Pisum*. *Sinapis* and *Raphanus* were found to grow better in pure oxygen, but more poorly in compressed air, while indifferent gases, such as hydrogen and nitrogen, worked unfavorably under increased pressure, as did also the reduction of the air-pressure below the normal. Peas and other plants grew in air richer in oxygen just as well as in ordinary air.

Montemartini (1892) observed that seedlings of spinach grew best in 4 per cent CO_2, less well in 7 per cent, and poorly in 22 per cent. Those of *Tropaeolum* grew vigorously in 4 per cent, poorly in 7 per cent, and perished in 22 per cent. The roots of peas grew slightly better in 4 per cent CO_2 than in normal culture, while growth was considerably retarded at 7 per cent and reduced more than half at 22 per cent. The higher amounts of carbon dioxid called forth striking modifications in leaf-structure. The thickness of the palisade increased in relation to the sponge parenchyma; its intercellular spaces were smaller and the cells narrower.

Jentys (1892 : 306) cultivated beans, wheat, rye, and lupines in glass jars under the influence of varying amounts of CO_2, namely, 4, 5, 8, and 12 per cent. The action of such mixtures was less injurious than would be assumed from Böhm's results. In periods of

31 to 64 days, beans showed not only a quantitative decrease in the wet and dry weight of shoots and roots, amounting in the case of the latter sometimes to nearly one-third, but they were also shorter and more bushy, with fewer rootlets. The roots of lupines and rye in a mixture of 5 per cent CO_2 were both more shallow and less developed, while the roots of wheat were practically indifferent to the gas.

Jaccard (1893 : 289) found that rarefied air brought about an acceleration of growth, accompanied by modifications in the general aspect of the plant, while air compressed between 3 and 4 atmospheres frequently produced an acceleration of growth which was weaker and less general than in the case of rarefied air. Its injurious effect did not occur until a pressure of 8 atmospheres was reached. When oxygen was added up to 90 per cent, there was in general no injurious effect upon growth, and if such air was rarefied it brought about an increased rate of growth. When a mixture containing 70 per cent of oxygen was compressed until the oxygen tension equaled that of 10 atmospheres of air, growth was greatly hindered.

Chudiakow (1894 : 333) investigated the effect of temperature upon the length of life in the absence of oxygen, using young seedlings of *Vicia faba*, *Triticum vulgare*, *Pisum sativum*, and *Helianthus annuus*. The results showed that the increased respiration due to higher temperature did not make the plants more resistant to the consequences of the withdrawal of oxygen. On the contrary, in spite of the greater rate of respiration or even on account of it, the plants died much more rapidly than at low temperatures. Experiments with swollen seeds of *Brassica napus*, *Triticum vulgare*, *Vicia faba*, and *Zea mays* gave the same results.

Recent researches.—In the case of roots of *Vicia sativa* and *Pisum sativum*, Chapin (1902 : 375) observed that the slowing-down of growth was noticeable at 5 per cent CO_2 and growth stopped completely at 25 to 30 per cent. An injurious after-effect was not noticed when 20 per cent CO_2 acted for 120 hours. At 40 per cent no significant damage was noticed after 24 to 28 hours, but if the plants remained 72 to 96 hours in 20 to 40 per cent CO_2, the after-effect became evident. The formation of lateral roots was completely suppressed in 20 to 25 per cent CO_2. Seedlings of *Pisum sativum* were unable to develop at 20 per cent and were killed at 25 per cent in 96 hours. The corresponding values for *Vicia sativa* were 35 per cent and 80 per cent in 40 hours. The hypocotyl of *Sinapis* and *Trifolium* began to stop growth at 15 per cent and completely ceased to grow at 25 per cent. The time necessary to kill plants in CO_2 decreased as the content increased. With roots and shoots a small amount of growth was still evident after 24 hours with all the higher percentages of CO_2, and the effect of the gas therefore was not instantaneous. There was a great difference in the resistance to

carbon dioxid between flowering plants and fungi. The first were killed by long immersion in 20 to 30 per cent CO_2, while the fungi could not be entirely killed in any intensity. With the former the growth stopped at 20 to 30 per cent, with the fungi at 40 to 80 per cent. The optimum amount of CO_2 for the growth of the higher plants studied was about 0.5 per cent. Carbon dioxid in small amounts acted as a stimulus, but in greater amounts as a poison.

Nabokich (1903 : 272) combated the views of Wieler and of Godlewski and Polzeniusz as to the suppression of growth in the absence of oxygen. He found that hypocotyl of sunflower, 48 to 49 mm. long, made an average growth of 6.3 mm. during 35 hours in pure hydrogen, while another set gave an average of 4.8 mm. during a 36-hour culture. Seedlings were also grown in a series of containers of about 100 c.c. volume, with different amounts of oxygen for 20 hours with the results shown in table 25.

TABLE 25.

O.	Average growth.
c.c.	*mm.*
none	0.9
0.02	1.3
0.04	1.0
0.06	0.8
14.	6.2
Unlimited	9.0

In a later paper (1909 : 51), the same author has given an extensive and unsympathetic account of the work of other investigators upon growth in the absence of oxygen. The authors considered were Borodin, Pfeffer, Wortmann, Detmer, Möller, Wieler, Palladin, Pringsheim, Clark, Correns, Chudiakow, Iwanowsky, Jodin, Kühne, Celakowsky, Ritter, Mazé, Godlewski and Polzeniusz, Polowzow, and Dude. In addition to extending his earlier studies of growth, he found that shoots of *Pisum* exposed to oxygen-free media for 5½ hours showed all the stages of mitosis, just as in the control shoots, but that in 50-hour exposure, all nuclei were in the resting-stage except those that had dissolved, probably as a result of the death of the protoplasm. He concluded that anaerobic growth in certain relations is completely identical with normal aerobic growth. This is chiefly shown by the fact that the development of plants in oxygen-free media takes place in accordance with the usual rules, that the plants retain the ability to respond to external stimuli, such as gravity, in the ordinary manner, and that the growth of tissue results from the formation of cells by normal mitosis. On the contrary, other phenomena are in disagreement with normal aerobic growth. These are the universal death of cells in oxygen-free media, the peculiar course of the curve of growth in different periods, and the specific dependence of growth upon the temperature and upon the sugar solutions.

Mitscherlich (1910 : 158) has studied the effect of increasing the CO_2-content of the soil upon the production of oats, and finds that it has no effect in increasing the harvest. He thinks that the amount of CO_2 in the soil derived from the roots and from the composition of humus is so great that the solubility of nutrients can not

be increased by greater amounts. While he found that the use of CO_2 has no effect upon the harvest, it seemed that in some cases the development of roots was small.

Lehmann (1911 : 90) showed that many plants, e. g., *Vicia faba*, *Brassica napus*, *Lupinus albus*, *Pisum sativum*, and *Cucurbita*, stop growth very quickly when oxygen is withdrawn and are unable to grow even in sugar solution. He found no growth in epicotyls at 0.5 mm. pressure, though in some cases, e. g., *Helianthus annuus*, slight growth occurred in 0.5 to 1 per cent sugar solution at 20° C., and in distilled water at 25° C.

Crocker and Davis (1914 : 312) have shown that seedlings of *Alisma plantago* grew 30 to 32 mm. in 21 days in vacua, or 11 to 12 times the length of the embryo, while those in the air grew 50 to 57 mm. or 18 to 22 times the length of the embryo. No leaf branches were formed in the seedlings grown in vacua, and chlorophyll did not develop. With the air-pressure below 5 mm. no chlorophyll developed within a month. In the dark, an air-pressure of more than 15 mm. was needed to develop leaf branches. The formation of the primary root seemed to be dependent upon oxygen, as seedlings in drop cultures and on the surface of water produced primary roots, while few showed them beneath a layer of water, and none in an air-pressure much below 5 mm.

Cannon (1916 : 75) determined that the exposure of roots of *Prosopis* and *Opuntia* to pure carbon dioxid for 15 minutes did not affect growth, but exposure during periods of over 30 minutes inhibited it. Growth began again soonest after the shortest exposures, and sooner at high than at low soil temperatures. Roots of *Prosopis* recovered their normal rate of growth more readily than those of *Opuntia*. In later studies upon the effect of low percentages of oxygen (1917 : 82; 1918 : 82), he found that root-growth stopped sooner in *Opuntia versicolor* than in *Prosopis juliflora*, as shown by table 26.

TABLE 26.

Oxygen in soil-air.	Root-growth in days.	
	Opuntia.	Prosopis.
p. ct.		
0. (Nitrogen)	0	4 to 6
2.67.....	0 to 1	1 to 5
4.50.....	0 to 2	2 to 5
7.00.....	1	2 to 5
10.00.....	4 to 5	9 to 11

Root-growth regularly ceased in nitrogen, though it continued in some cases for a day or two (1919 : 71). The effect upon the shoot was less marked, in *Eriogonum* growth continuing at a rate of 8 to

15 mm. per day for the 8 days the roots were subjected to nitrogen. Shoots of potato, on the contrary, stopped growing very soon after the access of nitrogen. Growth was decreased in the case of morning-glory, tomato, and corn. Carbon dioxid in mixtures containing 25, 50, and 75 per cent exerted a depressing effect upon root-growth in *Krameria canescens*, and growth ceased after a time, to be renewed upon the re-entrance of air. In *Covillea* the effect was very harmful, growth being quickly retarded and soon ceasing. It was renewed but slowly in the air. In *Mesembryanthemum* growth was decreased, but it ceased only after relatively long exposures, and was renewed with relative rapidity. The difference in sensitivity to carbon dioxid was shown by the fact that the root-growth of *Covillea* ceased in 1.5 hours in 25 per cent CO_2, that of *Krameria* in 2.5, and of *Mesembryanthemum* in over 4 hours.

Experiments with such low amounts of oxygen as 2 and 1 per cent and with nitrogen (1920 : 60) again demonstrated the varying sensibility of different species. With 2 per cent oxygen, root-growth stopped promptly in the case of onion, and was much retarded in most of the other species. However, in the plants of wet soils, *Juncus*, *Potentilla*, and *Salix*, and in the succulent *Mesembryanthemum*, as well as in alfalfa, growth was decreased but slightly. In 1 per cent oxygen, growth ceased quickly, though in the species of wet soils and in *Mesembryanthemum* growth continued for several days. In commercial nitrogen root-growth continued for over 5 days in *Mesembryanthemum*, over 7 days in *Juncus* and *Potentilla*, and for 13 days in rice, while it was inhibited in the other species.

Cannon and Free (1919 : 86) have shown that the root-growth of the sweet-pea stopped at once in static atmospheres of nitrogen or helium, but continued for 3 days in a stream of helium at a rate little below normal growth in air. Injury to potato roots took place sooner in nitrogen than in helium. In later experiments (1920 : 61), this difference in the action of nitrogen and helium was confirmed, though it does not occur when conditions are entirely anaerobic or when an ample amount of oxygen is present. With nitrogen, 1.5 per cent of oxygen is required for the root-growth of the garden pea, but with helium 0.5 per cent suffices. Similar differences have been found in the germination of peas, the greening of rice seedlings, leaf movements in acacia and oxalis, stigma movements of *Diplacus glutinosus*, etc. It is suggested that this difference is due to the fact that oxygen diffuses more rapidly through helium than through nitrogen.

Kidd (1919 : 248) has shown that 5 to 10 per cent of oxygen is the optimal amount for the sprouting of potato tubers. Above this it is harmful, while 80 per cent inhibits it in 4 to 5 weeks. Its injurious effect is increased in the presence of carbon dioxid. The latter inhibits sprouting at 20 per cent, and higher concentrations cause marked injury and death.

Summary.—The general rule that growth is decreased or prevented by the absence of oxygen appears to suffer but a single exception. Jaccard stated that rarefied air brought about an acceleration of growth accompanied by modifications in aspect, but it seems probable that this was due to elongation and did not involve an actual increase in dry weight. Saussure found that most plants and plant organs died in a vacuum in the absence of sunlight, and explained the exceptional behavior of marsh-plants as due to the large amount of oxygen in their tissues. Crocker and Davis have shown that seedlings of *Alisma* grow considerably in vacua, but that this is little more than 50 per cent of their aerobic growth. Saussure, Jentys, Cannon, and Cannon and Free have found pure nitrogen to stop growth quickly or to greatly retard it, except in marsh-plants, and helium has much the same effect. Detmer and Palladin obtained no growth with seedlings in hydrogen, and Wilson noted that a mixture of nineteen-twentieths hydrogen and one-twentieth air produced a marked decrease, while Jentys likewise found this gas unfavorable to growth. Bert, Wieler, Jentys, Lehmann, and Crocker and Davis have all demonstrated that reduced air-pressure retards or inhibits growth, and Nabokich and Cannon have obtained the same results with amounts of oxygen of 2 per cent and below.

While pure oxygen or air-pressures of several atmospheres have generally been shown to retard growth, Bert, Jentys, and Jaccard have all observed exceptions to the rule. It is certain that both the species and the time of exposure account for very wide variations in response. Carbon dioxid naturally produces the same effect upon growth that it does upon germination, and all investigators are in accord in finding it very injurious. As a rule, the amount required to cause injury in mesophytes ranges from 5 to 10 per cent, but in hydrophytes and some xerophytes especially, it may be as high as 20 per cent, and, in exceptional cases, even higher.

The question of the possibility of the growth of phanerogams in the continued absence of oxygen has been discussed chiefly by Wieler, Nabokich, Godlewski and Polzeniusz, and Lehmann. While Nabokich has maintained that growth can regularly occur in the absence of oxygen, he is forced to admit that it differs from normal aerobic growth in its dependence upon sugar solutions and upon temperature, and in the universal death of the cells in oxygen-free media. His own experiments are hardly free from criticism, as he has taken no account of the air contained in the seedlings at the outset, which might well be enough to meet the exceedingly low requirements of the sunflower, as shown by Wieler. Moreover, it would seem difficult to prove that the small amounts of growth observed were not due to imbibition or turgor forces, as suggested long ago by Saussure. Finally, the most significant result was the death of 63 per cent of the seedlings at the end of a period of 34 to 36 hours without oxygen.

Consequently, the question of a short period of anaerobic growth under special conditions has little more than academic value. Even if shown to exist beyond question, it would be without significance for the functioning of organs or the growth of plants.

PROTOPLASMIC STREAMING AND MITOSIS.

Corti (1774 : 210) placed *Chara* in a vacuum under an air-pump and left the plants for 48 hours. The movement of protoplasm in the cells ceased, but began again in 8 to 12 hours after the plants were returned to atmospheric air. On the contrary, Dutrochet (1838 : 31) found that movement continued for 22 days under similar conditions, but Hofmeister (1867 : 49) was able to refute his conclusions by repeating Corti's experiments. Kabsch (1862 : 341) observed that protoplasmic movement in stamen-hairs of *Tradescantia* ceased after 45 minutes in CO_2, but in air it returned after 15 to 20 minutes. After 24 hours in CO_2 the protoplasm became coagulated and was no longer capable of response. The assumption was made that the cessation of movement was due to the lack of oxygen rather than to the direct effect of carbon dioxid. Kühne (1864 : 88, 104) also showed that there was no protoplasmic movement in the absence of air or in an atmosphere of hydrogen or CO_2. This held also for *Myxomycetes,* which showed no movement and no development in the absence of oxygen.

Frank (1872) kept shoots of *Elodea* under oil for several days, and found that movement ceased, to begin again with access of oxygen. Möller (1884) found that nitrogen stopped the movement of protoplasm in *Elodea* in 1 to 2 hours when the leaves were placed in the dark, and that the protoplasm finally contracted under longer exposure. He concluded that all gases, with the exception of oxygen and air, had an injurious effect, while some of them were actually poisonous.

In a study of protoplasmic movements in the absence of oxygen, Pfeffer (1887) reached the conclusion that not only movement but photosynthesis also was suppressed in the absence of free oxygen. He found some movement for a time after the withdrawal of oxygen and explained this as a result of minimal amounts which could not be absolutely excluded.

Clark (1888 : 273) observed that the streaming of the plasmodia of slime-molds ceased in the absence of oxygen in a few minutes, and readily began again upon the access of air. The complete withdrawal of oxygen also stopped the movement in *Triania* and *Urtica,* but it was renewed under a pressure of 1.2 mm. and 2.8 mm. respectively. In the case of flagellate forms, such as *Euglena,* the withdrawal of oxygen produced a resting-stage in the zoospores in a few minutes. With *Stylonichia,* a pressure of 2.5 mm. caused the individual to come to rest and to flatten out, while an increase of the

pressure to 6 mm. caused the latter process to cease, and the animal began to move again.

Hauptfleisch (1892 : 219) pointed out that protoplasmic streaming naturally ceased in the absence of oxygen, since this reduces the activity of aerobic plants, and movement is likewise renewed with the access of oxygen. He stated that streaming in the root-hairs of *Trianea* was gradually brought to a stop when hydrogen was led into the moist chamber.

Demoor (1894 : 163) studied the effects of different gases, of vacua, and cold upon living cells under the microscope. The plant material consisted of stamen-hairs of *Tradescantia*, plasmodia of *Chondrioderma difforme*, and chloroplasts of leaves of *Funaria*. Carbon dioxid brought streaming in the stamen-hairs to a stop in 3 to 6 minutes, but the mitotic process continued. However, no cell-wall was formed, unless conditions permitted the renewal of motion. Carbon dioxid stopped the activity of the chloroplasts of *Funaria* and killed the leucocytes of the blood in 2 to 3 hours. In hydrogen the protoplasm assumed a granular condition, and after 15 to 40 minutes movement was no longer visible. Oxygen increased the activity of the protoplasm and its movement. The author's view is that both carbon dioxid and hydrogen hinder respiration by withdrawing oxygen and stopping the protoplasmic movement. The former is the more injurious, because of its poisonous effect. He assumed that the activity of the nucleus is independent of that of the protoplasm, inasmuch as it can continue after the conditions are no longer favorable to the life of the protoplasm.

Lopriore (1895 : 547) found that CO_2 stopped the movement of protoplasm for a time, but did not have a permanently injurious effect, and concluded that its influence is specific and not due alone to the absence of oxygen. When CO_2 was mixed with 10 or 20 per cent of oxygen, the streaming was not long suppressed. It accommodated itself gradually to a high content of CO_2 and finally was not inhibited in nearly pure gas. Pure oxygen sometimes exerted a stimulating effect upon slow streaming, but not upon movement of normal rapidity. Pure hydrogen at first hastened movement, but later slowed it down markedly without entirely stopping it.

Celakowski (1892) found that movement of the protoplasm continued in cells of *Tradescantia* engulfed by the plasmodium of a slime-mold, indicating that the cells were supplied with oxygen. He also showed that movement could take place in the absence of oxygen in a number of one-celled and several-celled organisms. In contrast to his earlier results, Kühne (1898) observed that protoplasmic movement sometimes persisted for 1 to 3 weeks in the absence of oxygen. Ritter (1899) confirmed the observations of Kühne and Celakowsky upon anaerobic movement in the *Characeæ*, and recognized that sugar promoted movement and growth in bacteria facul-

tatively anaerobic. He was unable to find either growth or tropistic movement under the total exclusion of oxygen.

Samassa (1900 : 320) confirmed Lopriore's observation that pure oxygen did not increase the rate of protoplasmic movement in the stamen-hairs of *Tradescantia*. The lack of oxygen stopped the movement quickly, and in nitrous oxid it ceased in 15 to 20 minutes. In agreement with Lopriore, he found an adaptation to carbon dioxid, when successive mixtures were employed with more CO_2 and less oxygen, but in all cases pure carbon dioxid caused the motion to cease. The action of CO_2 was considered to be that of an acid, since the normal resting nucleus assumed the same foamy appearance noted in dilute solutions of sulphuric, acetic, and formic acids. The conclusion was reached that the cessation of motion due to the withdrawal of oxygen also stops mitosis, contrary to the observations of Demoor.

Pfeffer (1900 : 546) called in question Kühne's assumption that the streaming of the protoplasm of *Nitella* for 50 days in darkness was due to traces of oxygen in the protoplasm, and thought the proper explanation to be that *Nitella* is a partial anaerobe. He regarded the whole matter as demanding more study, since Ewart has shown that a minute trace of oxygen is sufficient to maintain movement in *Chara* almost indefinitely.

Sabline (1903 : 488) found a considerable number of mitotic figures in root-tips of *Vicia faba* deprived of oxygen for a period of 2 hours. The figures were more or less modified, chiefly by the absence of the formation of a cell-plate and the faintness of the spindle.

O. Nabokich (1904 : 62) subjected young seedlings of *Helianthus annuus*, *Pisum sativum*, and *Phaseolus vulgaris* to an oxygenless atmosphere for 5 to 51 hours. Her chief conclusion was that a normal anaerobic mitosis occurs with some higher plants. In the young leaves and growing-points of sunflower all mitotic stages were found in the cultures for 5, 18, 23, 30, and 43 hours, while with 50 hours no figures were seen. The buds of pea and bean behaved similarly, though mitotic figures disappeared earlier. Pea roots were much more sensitive, the figures disappearing after 20 hours, while in root-tips of the bean practically none were found after 5 hours. In nearly all cases the cell-wall was formed normally in *Helianthus*, but it was suppressed after 5 hours in *Phaseolus*. The author concluded that cell-division is independent of the presence of oxygen, and that the injury observed was due to secondary influences.

Andrews (1912 : 473) found that hydrogen stopped protoplasmic movement in *Mucor mucedo* and *M. stolonifer* in 20 minutes in moist air, while Schröter found 5 minutes sufficient. In dry air it required 54 minutes for hydrogen to stop the movement. In this case, 5 minutes were required for streaming to begin again instead of 1 minute after moist air.

Summary.—The absence of oxygen stops the movement of protoplasm in all plant-cells studied, with the possible exception of *Nitella*. This is equally true whether the air be removed by exhaustion, replaced by hydrogen, or its access prevented in various ways. Since Ewart has shown that exceedingly minute quantities of oxygen suffice for streaming in *Chara*, it is probable that this is likewise the case with *Nitella* and that the movement in the latter is not really anaerobic. Carbon dioxid and nitrous oxid inhibited protoplasmic movement in every instance, but both Lopriore and Samassa found a gradual accommodation to the former, so that higher and higher percentages were required to check streaming. As to the effect of an increased oxygen-content, Demoor thought that movement was promoted by it, but Lopriore found this to be true only of slow streaming, and Samassa obtained no increase at all.

With respect to the movements involved in mitosis, Demoor observed that mitotic processes continued in the stamen-hairs of *Tradescantia* after carbon dioxid had caused streaming to cease. No cell-plate was formed, however, and division remained incomplete as long as movement was impossible. He concluded that the activity of the nucleus is independent of that of the protoplasm, but it seems that this can be but partially true at most, since mitosis is imperfect in the absence of oxygen, and streaming comprises but a part of the protoplasmic activity.

Sabline obtained similar results with root-tips of *Vicia* grown without oxygen, the cell-plate being absent and the spindle faint, while Samassa found that the withdrawal of oxygen inhibited mitosis as well as movement. This discrepancy may be explained by the results of O. Nabokich, who found that different plants and different parts of the same plant varied much in sensibility to the lack of oxygen. Mitotic figures disappeared in the sunflower only with 50 hours' exposure, but earlier in the buds of pea and bean, while in root-tips of the pea they were absent after 20 hours and in those of the bean after 5 hours. In most cases the cell-plate appeared in the sunflower, but it was suppressed after 5 hours exposure in the bean. The conclusion that nuclear division is independent of oxygen and that the injuries observed were due to secondary factors does not seem to be warranted by the facts. It seems not improbable that mitosis is still possible in the presence of minute quantities of oxygen, as Ewart has shown for streaming in *Chara*, and that such amounts may have persisted in the tissues for the relatively short periods of exposure. This explanation is supported by Pfeffer's observation that movement continued for some time after the exclusion of oxygen.

IRRITABILITY.

The first observations upon the relation of oxygen to irritability were those of Dutrochet (1838), who found that the leaflets of *Mimosa pudica* folded together with the beginning of air exhaustion,

and with further pumping partially unfolded. After 2 hours in the receiver the plants responded again to mechanical stimulus, but with 12 hours in vacuum their irritability had disappeared. The leaves of *Mimosa pudica* failed to show sleep movements, and the heads of *Leontodon taraxacum* and *Sonchus oleraceus* were unable to close or to open in rarefied air, while "sleeping" leaves of *Robinia pseudacacia* did not open in water free from air.

Payer (1842 : 1194) found that seedlings of *Lepidium sativum* exhibited distinct phototropic curvatures in hydrogen or nitrogen, as well as under water, but these were reduced in degree.

Kabsch (1862 : 341) investigated the effect of carbon dioxid and other gases upon irritability. In pure CO_2 the sensibility of filaments of species of *Berberis* to mechanical stimuli ceased almost instantly. It returned in the air after a few minutes, when immersion in the CO_2 had lasted not more than 5 to 10 minutes, but only after several hours when immersion had lasted for 3 to 4 hours. Even after 6 to 12 hours receptivity had not completely disappeared. A mixture of 30 to 40 per cent of carbon dioxid with air was without effect, but irritability disappeared under greater amounts. The inflorescence of *Berberis* developed buds and flowers normally after 2 to 3 days in pure CO_2, but a longer stay produced ill effects. *Oxalis acetosella* and *O. corniculata* in carbon dioxid failed to show the normal sleep movements of the leaflets. After being brought into the air, the movements were not resumed until 3 days had elapsed. Movements of the leaflets occurred at a pressure of 15 mm., but at 2 to 3 mm. they were no longer irritable. The leaves of *Oxalis* and the heads of *Bellis* suspended their periodic movements in vacua, but resumed them upon renewed access to air.

Wiesner (1878 : 58) subjected seedlings of *Lepidium sativum*, *Phaseolus multiflorus*, *Sinapis alba*, and *Vicia faba* to an atmosphere free from oxygen. No curvature occurred after exposure to the light for several hours, but when air was permitted to enter it became visible in an hour. His conclusion was that heliotropism is impossible in the absence of oxygen.

Wortmann (1879:509) placed germinating seeds of *Phaseolus multiflorus*, *P. vulgaris*, and *Vicia faba* in an oxygen-free atmosphere, which completely inhibited geotropic curvature in the horizontal roots, as well as in the stems of *Pœonia peregrina*. He stated that irritability is entirely lost when oxygen is lacking, but that it returns with renewed access, even after deprivation for weeks. In a special study of geotropism (1884 : 705), seedlings of *Helianthus*, *Lepidium*, and *Phaseolus* were placed in a partial vacuum. The slight curvature already begun ceased after a short time, and could not be again induced by the admission of air. Shoots exposed to hydrogen in a horizontal position exhibited no geotropic after-effect when placed in the air, in spite of further growth in length. Detmer

(1881) confirmed the results of Wortmann, finding that heliotropism and geotropism in *Pisum* and *Triticum* were suppressed by nitrogen, hydrogen, and CO_2.

Kraus (1884 : 199) exposed horizontal flower-shoots of *Anthriscus, Ranunculus, Taraxacum,* etc., to streaming carbon dioxid and hydrogen. After 6 hours no geotropic effect was visible, but upon exposure to the air curvature took place in 5 hours. He regarded this as proof that the plants merely pass into a state of rigor.

Correns (1892 : 87) made an exhaustive study of the relation of irritability to the presence of oxygen, and at the same time considered the results of Kabsch and Dutrochet. He observed that, at sufficiently low pressures, rigidity occurred, the petiole rising and the leaflets closing toward each other. According to Kabsch, reduced pressure effected a movement of the stamens in *Berberis* and *Mahonia,* results verified by Correns. The latter showed also that both hydrogen and nitrous oxid gave similar results, while the sudden increase of the air-pressure did not act as a stimulus. After a period in hydrogen irritability ceased. In pure oxygen the filaments of *Berberis* did not react, but they remained irritable after 24 hours' immersion. Both Kabsch and Correns found that the filaments did not react to CO_2, 50 per cent CO_2 destroying irritability in 10 minutes. The stigmatic lobes of *Mimulus* closed under reduced pressure, as they did also in hydrogen. In pure oxygen the stigmas retained their irritability as long as 48 hours. The leaves of *Securigera, Tetragonolobus, Oxalis, Lupinus, Trigonella, Medicago, Trifolium,* and *Amicia* lost their irritability under reduced pressure, both night closing and morning opening being suppressed. *Oxalis* was unable to withstand the lowered pressure and was completely dead after 12 hours. For the appearance of sleep movements in *Oxalis,* 3.5 per cent of the oxygen originally present was necessary; for *Securigera,* 5 per cent closed the leaves quickly, while it acted more slowly for *Tetragonolobus.* Sleep movements ceased in pure hydrogen, as they did in CO_2, nitrogen, and nitrous oxid. Correns confirmed the discovery of Wortmann that geotropic movements were suspended in vacua, and that of Wiesner, which gave similar results for heliotropic movements. He also corroborated the results of Wieler as to the cessation of growth in the absence of oxygen. He noted that the growth of shoots ceased before that of seedlings, and that shoots of *Helianthus* died at 1 per cent of the original amount of oxygen, and *Vicia* at 2 per cent.

Reduction of the pressure did not produce reaction in tendrils, though they responded slightly to contact in oxygen-free air. For distinct response the lowest limit was 3 to 4 per cent for *Passiflora, Sicyos,* and *Bryonia,* and 2 to 3 per cent for *Cyclanthera.* In a mixture of 12 per cent air and 80 per cent CO_2, irritability was lost in a short time. Reduced pressure did not produce reaction in the

tentacles of *Drosera*, but the power to perceive stimuli and to respond persisted in the presence of the minutest quantities of oxygen.

Czapek (1895 : 274) showed that geotropic induction is possible in lupine seedlings placed in a vacuum and then in hydrogen, although no growth took place.

Paal (1912 : 1) noted the time required for the geotropic curvature of bean roots at different air-pressures, and found that the reaction-time was lengthened by reduced pressure. Further experiment showed that the presentation-time was also increased by decreasing pressure, gradually at first and then very rapidly.

Kenkel (1913) studied the effect of reduced air-pressure upon irritability, and found that the geotropic reaction still occurred at an oxygen-content at which heliotropic curvature was no longer possible.

Van Ameijden (1917 : 211) has carried out a comprehensive investigation as to the irritability of *Avena sativa* in an oxygen-free atmosphere obtained by means of nitrogen. He finds that when seedlings, long enough removed from the effect of oxygen, receive geotropic or heliotropic stimuli in the absence of oxygen and are placed at once in the air, they are unable to react. Reaction does occur, however, after a similar fore-period, if the seedlings are both stimulated and left in the air. In the absence of oxygen the perception of a stimulus can not take place if there has been a sufficiently long fore-period. After the perception of a stimulus the seedlings do not react if left in an oxygen-free atmosphere, showing that oxygen is necessary for the reaction. Seedlings retain the power of perception for a long time in a low oxygen-content, but this is weakened by a prolonged stay. Complete or partial withdrawal of oxygen produced no difference in the reaction of seedlings to geotropic or heliotropic stimuli.

Summary.—Practically all tropistic responses are suppressed in the absence of oxygen, though reaction to contact may persist in the presence of minute quantities. The relation of geotropism to oxygen has been studied by Wortmann, Detmer, Kraus, Correns, Czapek, Ritter, Paal, Kenkel, and Van Ameijden, and all are in agreement that geotropic curvature is impossible without oxygen, whether this is secured by means of a vacuum or by the use of hydrogen, carbon dioxid, or nitrous oxid. Wiesner, Detmer, Correns, Kenkel, and Van Ameijden have shown that heliotropic response is similarly inhibited. The nyctotropic movements of leaves and the anthotropic ones of flower-heads have been found by Dutrochet and Kabsch to cease in a vacuum, as well as under greatly reduced pressure or in carbon dioxid. Correns obtained the same result with the leaves of several genera under reduced pressure, or in pure hydrogen, nitrogen, carbon dioxid, or nitrous oxid, and both Kabsch and Correns observed that the irritability of stamen filaments was suppressed by carbon dioxid.

FUNGI.

Humboldt (1793) was the first to state that agarics gave off hydrogen during respiration, and DeCandolle (1832) later determined that *Sphœria* and *Peziza* exhaled hydrogen when exposed under water to sunlight.

Marcet (1829, 1834) found that fungi excreted a small quantity of CO_2, but no hydrogen, in bell-glasses containing air. When placed under water, however, they rapidly disengaged both nitrogen and hydrogen in sunlight as well as in darkness. In his later experiments the respiration of fungi was studied in the air, in oxygen, and in nitrogen. In every case a certain amount of CO_2 was obtained, abundantly in the case of oxygen and less so in that of nitrogen. In these experiments no generation of hydrogen occurred, and, contrary to his preceding opinion, he admitted that the hydrogen was produced by the beginning of decomposition.

Pasteur (1861, 1876) was the first to show that yeast and certain bacteria could grow in the absence of oxygen if a supply of energy was available, but that anaerobic growth was not indefinitely possible, in the case of yeast at least.

Brefeld (1874, 1876) found that yeast was still capable of development in an atmosphere of CO_2 which contained one six-thousandth part of oxygen. Yeast was shown to possess the ability to grow without free oxygen in the midst of sugars, which were fermented to CO_2 and alcohol. The limit of growth occurred at 12 per cent and that of fermentation at 14 per cent of alcohol. A similar ability was exhibited by *Mucor racemosus*, but the fermentation proceeded more slowly under similar conditions, and the respective limits of growth and fermentation were 4.5 and 5.5 per cent of alcohol. In the case of *Mucor stolonifer* the fungus produced fermentation without growing and became inactive at 1.5 per cent of alcohol. He concluded that in the case of all plants, from the simplest to the highest, abnormal decompositions occur in the absence of oxygen, which, in certain respects, such as the constant formation of CO_2 and alcohol, are in harmony with the alcoholic fermentation of yeast.

Selmi (1874) observed the evolution of hydrogen from molds and from *Agaricus cæsarea* and supposed that this occurred also in the presence of free oxygen. Gugini (1876 : 111) pointed out that this was due to the use of sulphur or arsenic in the experiment, while Missaghi (1875) found no hydrogen when moulds grew in atmospheric air.

Müntz (1876 : 67) determined that *Agaricus campestris* produced no hydrogen in atmospheric air constantly renewed. When, however, this mushroom was placed in an atmosphere without oxygen, it produced a small quantity of hydrogen, as well as large amounts of CO_2. He stated that all fungi in an atmosphere without oxygen transform the sugars which they contain into alcohol and CO.

When the sugar is mannite this transformation is accompanied by the evolution of hydrogen, and this is notably the case whenever bacterial decomposition sets in.

Sadebeck (1881) observed that the spores of *Ascomyces tosquinetii*, when placed in a sugar solution in the complete absence of oxygen, exhibited an extraordinarily energetic germination, even better and more rapid than in the air.

Foth (1889 : 279) observed that carbonic acid, like other acids, exerted a strong limiting action on the budding of yeast, and that its fermentative activity was influenced by even small amounts, while different races of yeast were resistant to CO_2 in varying degrees.

Fränkel (1889 : 332) found carbon dioxid to limit the growth but not to kill rose yeast and black yeast, while the true yeasts thrived in it. He divided the bacteria into several classes, namely, those which grow as well in CO_2 as in air, those which can develop in CO_2 but whose growth is greatly reduced by it, and those which can not develop at ordinary temperatures in pure CO_2, but can in incubation temperatures. The remaining bacteria, which are in general saprophytes, do not develop in CO_2, but are not killed by it, and they grow again when placed in air. Finally, there are bacteria which are killed in CO_2, among which are the most important pathogenic forms.

Frankland (1889 : 13) found the widest range of response to unfavorable conditions among one-celled organisms, the majority of individuals dying quickly, while a few remained unharmed.

D'Arsonval (1891 : 667) showed that carbon dioxid under a pressure of 45 atmospheres was a sterilizing agent of great significance, replacing the autoclave. While the resistance of the bacteria was very variable, all were killed after long treatment at a temperature of 40° C.

Freudenreich (1892 : 7) found that the anthrax bacillus and one other found in milk were resistant to a CO_2-pressure of 80 to 90 atmospheres and an oxygen-pressure of 60 atmospheres, combined with a rise of temperature to about 65° C.

Van Slyke and Bosworth (1908) have found that carbon dioxid under pressure exerts a marked retarding action upon the development of lactic-acid bacteria, to the extent that fresh milk so treated exhibits practically no increase in acidity after 9 months at 40° to 60° F.

Bosio (1893 : 61) stated that carbon dioxid under pressure suppressed the development of *Mycoderma aceti* and *M. vini* in beer.

Lopriore (1895 : 621) observed that spores of *Mucor mucedo* could not germinate in pure CO_2 when they remained in the gas 3 months, but that they would germinate and grow normally when again brought into air. He found, moreover, that spores germinated at 90 per cent CO_2 and that the number of germinated spores increased

with decreasing CO_2. Pure CO_2 stopped the growth of hyphæ in 24 hours. Mixtures which contained 10 to 30 per cent could neither suppress the growth of the hyphæ nor the production of the sporangia, but growth was much slower. A higher content of CO_2 checked growth and suppressed sporangia, but the latter developed when air was substituted. Bursting of the hyphæ occurred when cultures were exposed for several days to high CO_2-content. The higher the latter, the greater the number of vacuoles in the protoplasm. The propagation of yeast was inhibited in pure CO_2, but was resumed upon the replacement with air. *Mycoderma cerevisiæ* was much more susceptible, and it lost its power of propagation after a 12-hour exposure.

Ortloff (1900 : 763) found that the increase of yeast-cells was reduced by a stream of CO_2, but that the amount of the fermented sugar during 28-hour exposure was greater than in normal cultures.

Chapin (1902 : 375) found that the spores of *Mucor*, *Aspergillus*, and *Penicillium* did not germinate in a high content of CO_2, but after being exposed to pure CO_2 for 4 months, they were able to germinate when again brought into air. The amount of CO_2 necessary to hinder germination was 60 per cent for *Mucor* and 90 per cent for *Penicillium* and *Aspergillus*. Cessation of the growth of the hyphæ took place at 30 to 40 per cent for *Mucor* and at 80 per cent with the other two. The production of spores was hindered at 20 per cent in *Mucor*, 40 per cent in *Aspergillus*, and 50 per cent in *Penicillium*.

Kostytschew (1907 : 178) showed that the normal and anaerobic respiration of *Penicillium glaucum* and *Aspergillus niger*, when nourished with mannite, took place without the formation of hydrogen, and apparently without anything in common with alcoholic fermentation. He likewise found that in the case of *Agaricus campestris* the normal and anaerobic respiration of fungi containing mannite took place without the formation of hydrogen, and regarded it as clear that the hydrogen found by Müntz was due to the activity of bacteria. In a later publication (1907[2] : 188) he stated that no trace of ethyl alcohol was found during the anaerobic respiration of *Agaricus campestris*, and hence the process is distinct from zymase fermentation.

Summary.—Practically all the yeasts and molds and the great majority of bacteria are more or less aerobic in nature. They may live and even carry on certain functions for a time under anaerobic conditions, but growth for an indefinite period is impossible. In the soil especially it seems probable that many of them live and function under conditions alternately aerobic and anaerobic. A considerable number of bacteria are obligate aerobes, as well as some yeasts, and are able to withstand the absence of oxygen for but a short time. The obligate anaerobes are practically all bacteria, some of which

are able to grow aerobically under certain conditions. In fact, Beijerinck (1897) has called in question the existence of permanent anaerobes.

The bacteria, yeasts, and molds that produce fermentation are the commonest of temporary anaerobes, since their ability to use sugar enables them to dispense with free oxygen for a time (Smith, 1895). They differ greatly in their ability to live without oxygen, *Ascomyces* growing better than in the air, and some of the yeasts reproducing repeatedly in its absence, while the bread-mold soon ceases growth and becomes inactive. Fermentation may continue until stopped by the accumulation of alcohol, while growth ceases more quickly and reproduction still earlier.

Practically all fungi are affected by carbon dioxid, but to a much smaller degree than chlorophyllous plants. While a few bacteria and yeasts may grow more or less normally in pure carbon dioxid, the growth of the great majority is retarded or inhibited, and many are quickly killed by it. The common molds, *Mucor*, *Aspergillus*, and *Penicillium*, were unable to germinate in pure carbon dioxid, though the spores were not killed by an exposure of 3 months. In *Mucor* spore formation was stopped by 20 per cent CO_2, growth stopped at 30 to 40 per cent, and germination at 60 per cent, while for *Aspergillus* and *Penicillium* the respective percentages were 50, 80, and 90.

While the importance of the bacteria in the soil has been universally recognized, much less attention has been given to the molds and other fungi found in the soil. Waksman (1916) has recently summarized the investigations in this field and has given an account of his own studies (1917). He has isolated over 200 species of fungi from 25 different soils in North America and the Hawaiian Islands, representing the *Mucoraceæ*, *Sphæriaceæ*, *Mucedinaceæ*, *Dematiaceæ*, *Tuberculariaceæ*, and *Saccharomycetaceæ*. It appears certain that molds must play an important part in many soils, and especially in those with deficient aeration. While too little is known of their products under anaerobic conditions, there is no question that they produce organic acids and other substances that must be taken into account in connection with acidity and toxicity.

AERATION AS AN ECOLOGICAL FACTOR.

Sorauer (1873, 1886, 1895, 1909) was perhaps the first to thoroughly appreciate the importance of aeration in practice, doubtless because he has been the chief exponent of the non-parasitic diseases of plants. In the successive editions of his "Handbuch der Planzenkrankheiten" he has dealt with the effects of deficient aeration in detail. These are discussed under various captions, namely, lack of oxygen (1909 : 312), puddling of the soil (190), flooding and forswamping (195), souring of seeds and potted plants (201), excessive

watering (206), and deep planting of trees and seeds. The relation of aeration to growth and the treatment of soils to promote it are considered at considerable length in his "Popular Treatise on the Physiology of Plants" (1895 : 61), under the headings, "How can the soil best meet the requirements of the roots for air?" "How can we improve our fields so as to obtain the best possible crops?" "How is the nutrition of pot-plants effected?" and "How do ordinary roots obtain their necessary supply of air?"

Sorauer stated that plants without access of oxygen gradually die. When the living cells can absorb no more oxygen their functions undergo a change of direction; later they pass into a state of rigidity, in which movement of the protoplasm ceases, sensibility to stimuli is lost, and growth stops. However, the plants do not die immediately; they exhale carbon dioxid for a long time and can resume their functions upon renewed access of oxygen, even after apparent death. Sour soil is immediately recognized by its peculiar odor and a wholly different process of decomposition of the organic matter occurs in it. There probably arise acid combinations in the little-known series of humus compounds, in addition to the free acids formed. If iron is present, the harmless ferric salts may be reduced to the ferrous ones, since perceptible lack of oxygen must result from the filling-up of the soil spaces with water. Water filled with carbon dioxid derived from the root secretion as well as from the decomposition of organic matter alone suffices to kill plants after protracted action.

Vonhausen (1877 : 724) placed a clay drain-tube in the middle of a third of the length of a seed-bed sown with seeds of *Platanus*. The ends of the tube led out to the surface of the soil. At first the non-aerated portion showed no difference, but from the beginning of August the growth in the aerated portion was much greater both in height and in luxuriance. It was suggested that a similar method of aeration could be used in all nursery and seed-beds, and that it might be employed in vegetable gardening as well.

Böhm (1881) found an example of disease due to faulty aeration in the case of dying *Ailanthus* that had been planted too deeply in the Ringstrasse in Vienna. These trees had been diminishing in growth for a number of years, as the annual rings formed soon after planting were often more than 3 mm. wide, while those of the years preceding the death of the tree were but 0.5 mm. At the death of the trees the earth of the root-ball was so injurious that seeds of different plants quickly decayed when placed in it. The seeds readily developed, however, after the earth was repeatedly soaked with water and exposed in a thin layer to the action of the summer sun.

Wollny (1889[2]: 379) stated that in general the most important rule for agricultural practice was to increase the access of atmospheric air to the soil in the most complete manner possible. Soil in the powdery condition contains less air than a crumbly one, and the dif-

ference increases with increasing water-content. The soil of fields in the latter condition is significantly more permeable to air than one in the powdery condition.

Hartig (1894 : 275) pointed out the importance of oxygen for the roots of trees, and stated that the latter die from asphyxia if excluded from a constant supply. Physiological root-rot of pines and spruces is due to lack of soil-air, owing to the density of the soil or to its water-logged condition, and a similar root-rot occurs in plants grown in glazed pots. The remedy for both of these lies in better aeration of the soil. In beech woods the failure of natural regeneration is often due to poor aeration resulting from the thick layer of humus.

Warming (1895 : 96; 1909 : 43) regards soil-air as of the most fundamental significance to plants, since roots and underground shoots, like all other living parts, require oxygen for respiration. Plants adapted to ordinary soils are suffocated in very wet soils, and this results in alcoholic fermentation, followed by death and putrefaction. Soils poor in oxygen exhibit a different type of decomposition, and they become "sour" in consequence of the formation of great quantities of humous acids. The production of acid humus in the forest leads to the exclusion of air and the death of the trees. Ramann (1895, 1911) has likewise insisted that aeration is one of the most important of soil processes for the plant, since it has to do both with the access of oxygen and the removal of excessive carbon dioxid.

Mangin (1896 : 67) made a comprehensive study of the relation of the amount of CO_2 and oxygen in the soil-air about the roots of trees to the well-being of the latter. He found that soils which are packed are less aerated than other soils, and that the grills placed at the base of trees in porous soils were sufficient to assure good aeration. In compact soils or in consequence of watering, which makes the soil of the basin but slightly permeable, the renewal of the air by grills did not suffice to prevent the accumulation of CO_2 under the bitumen in quantities sometimes considerable. The watering of the basins presented serious difficulty in consequence of the compacting, which diminished the permeability of the soil to both air and water. While the aeration of the soil was very good in many places in the promenades, there were other places where the amount of CO_2 reached 8, 16, and even 24 parts per 100, while the oxygen was reduced as low as 15 or 10, or even 6 parts. Since CO_2 in the soil noticeably decreased growth, all of the trees found in the badly aerated soil slowly perished because of it, as well as owing to the lack of oxygen.

Dehérain (1896 : 468) reached the following conclusions with reference to the effect of tillage on aeration: Untilled soil is very well aerated. It inclosed as much air in the prairies and woods as when covered by spontaneous vegetation. Although the quantity of air

contained in tilled soils is greater than in untilled, the differences are insufficient to explain the value of tillage. Fallow mellow soil undergoes movements which increase the total amount of air-space. Rolling the soil diminishes its aeration.

Brizi (1906 : 89) regared the disease called "brusone" as being non-parasitic, at least in part, and probably due to irregular or incomplete respiration in water or soil low in oxygen.

Ehrenberg (1906 : 193) noted the case of turnips that had received so much liquid manure that the plants stood in water up to the crowns. At first they showed no injury, while the water was receding and being absorbed by the soil. Soon, however, a marked wilting developed rapidly among the leaves and finally extended to the petioles. For several days the leaves remained hanging and then gradually began to recover, although certain portions, especially at the tip of old leaves, died off. Later, similar observations were made on sugar-beets and carrots, while corn, grass, and other plants showed no injury from the flooding. The injury to fleshy roots was ascribed to the lack of oxygen, since these require a large amount at the time of their most active development.

Clements (1907 : 19) regarded air-content as a factor of importance in all soils, but particularly in acid ones, owing to the constant use of oxygen by the roots. The air-content varies inversely as the water-content, and hence water-plants show characteristic modifications called forth in response to a low air-content. Plants which grow in saturated soils or in water apparently do not compete for the latter, though it is probable that a new factor, air-content, enters the problem.

Hesselmann (1910 : 91) has emphasized the fact that the swamping of pine forests in Sweden is not a question of water, but of oxygen. The water of the moors and swamp forests is almost completely free from oxygen, and the pine forests suffer greatly in consequence. On the other hand, the pines thrive on the banks of spring brooks, where the water contains oxygen as a result of its rapid motion. In northernmost Sweden the swamping of the soil is gradually increasing through a marked rise in the level of the ground-water. The latter has been deprived of its oxygen through contact with the peat and thus brings about a significant depression of the functioning of the tree roots. Wherever the soil is better aerated or the motion of the water more rapid, so that it absorbs oxygen, the water works no injury, even though it had originally been rendered oxygen-free in passing through the moor.

Hole (1911) pointed out that the *Saccharum-Shorea* community in India grew in moist but well-aerated soil, while the *Erianthus-Terminalia* community occurred in soil moist to wet, and hence less aerated and apt to become somewhat water-logged during rains. *Shorea* was stated to be decidedly sensitive in regard to aeration

and was likely to establish itself only on well-drained soil not subject to water-logging.

Balls (1912 : 38) found that the roots of the cotton plant in Egypt were locally asphyxiated in water-logged soil, and in a few weeks even the stout woody roots were not merely dead, but also decomposed. When the depth of available soil was decreased by raising the water-table and thus asphyxiating or killing the lower part of the root-system, greater absorption was demanded of the surface roots. Excavations of a root-system which had been partially submerged in subsoil water showed all the original tap-roots and branches dead from 160 cm. to the maximum, 220 cm. This level coincided with the maximum height of the water-table, which had been maintained for 10 days at the end of September. Alongside of the brown and partly decomposed roots were new white roots in abundance, which ended at various depths up to 210 cm. These new roots were all found to arise from laterals which had not been reached by the water-table. With the fall of the latter, these healthy laterals had developed hundreds of rootlets that grew downward as the water receded.

Harrison and Aiyer (1913 : 106) have reached the conclusion that the surface film of algæ is the chief agent in the aeration of the roots of the rice crop. The oxygen evolved by the algal film is dissolved by the irrigation water to produce a highly aerated solution. In undrained soils this can not enter the soil, with the result that the roots are congested near the surface, thus limiting the area of root action. In drained soils the aerated water is carried downward, and the roots consequently penetrate to greater depths. The mass of soil subject to absorption is increased and the crop is correspondingly benefited. Too rapid drainage hinders the formation of the algal film and lessens the consequent aeration. The optimum rate of drainage for all swamp paddy soils is a comparatively slow one. This is due to the fact that aeration by atmospheric oxygen is less effective in promoting root aeration than that by the aerated water draining through them. The use of green manures in drained paddy soils promotes the activity of the algal film and thereby increases the aeration of the roots.

The studies of Hole and Singh (1914 : 10) upon aeration in forest soils in India show that lack of oxygen is a factor of great importance and wide extent. The general summary of their results is as follows (101):

"1. The present experiments have confirmed the results previously obtained regarding the very injurious effect of bad aeration on the growth of sal seedlings in the local forest soil.

"2. When water is long held in contact with this soil, which is the case under conditions of bad aeration, it becomes heavily charged with carbon dioxid and impoverished as regards its supply of oxygen.

"3. The bad growth of sal seedlings in this soil is correlated with an accumulation of carbon dioxid in the soil-solution and a low oxygen-content, and this possibly explains the evil effects of bad aeration. Further work, however, is required to prove this and also to decide the relative importance of carbon dioxid and oxygen, respectively.

"4. Liming this soil, immediately before sowing, has an injurious effect upon sal seedlings, and during the rains, soil which has been thus limed appears to contain more carbon dioxid and less oxygen than the unlimed soil. It seems possible that this may be due to accelerated bacterial activity.

"5. As carbon dioxid is rapidly dissipated and a deficiency of oxygen made good under the ordinary conditions of water cultures, it is not easy to prove the effect of varying quantities of these gases on plants grown in cultures. For the same reason artificial aeration of such cultures may not show any beneficial result.

"6 As sal seedlings can be successfully grown in water cultures, the injurious effect of bad aeration is not due to water as such This probably explains the fact that sal can grow on the banks of the rivers or even of stagnant lakes, in which the water is kept well aerated by exposure to the air or by the presence of green aquatic plants."

Bernbeck (1914 : 26) has pointed out the importance of fresh soil-air for the growth of tree roots and emphasized the relation of the amount of air in the soil to the porosity. Graves (1915 : 213) has studied a disease of coniferous seedlings growing in clay seedbeds. The disease caused most havoc during the wet months, while many cases of recovery occurred in the drier months. In porous soil, in the same nursery, the disease has never been known to occur, and he concludes that it is due to a lack of oxygen in a soil saturated with water.

Howard and Howard (1915 : 19) have concluded that the so-called disease of Java indigo in India is due to long-continued saturation of the soil, which leads to the death of the young absorbing roots, consequent leaf-fall, and more or less complete wilting. In dealing with soil ventilation (1915[2] : 35; 1915[3] : 11), they have discussed the relation between aeration and manuring, green manuring, fallowing, packing of the surface soil, earth mulches, rice cultivation, grass effects, simulated diseases, peach yellows, surface crusts, and the saving of irrigation-water. Of especial interest are the so-called natural aerators, plants such as *Cajanus indicus*, *Trifolium resupinatum*, "busunduk," and alfalfa, which serve to break up the soil by reason of deep-seated tap-roots or large laterals. They emphasize the fact that crops differ greatly in the air requirement of their roots. Gram is cited as an example of a crop that requires a great deal of air and but a moderate amount of water. Hence great care must be taken to secure and maintain the proper relation between air and water in the soil.

Howard (1916) has discussed the improvement in the aeration of field soils under surface drainage, and has given a résumé of the whole subject of aeration in another bulletin (1916[2]). In this it is

pointed out that water-logging during September reduced the production of wheat at Pusa somewhat more than 100 per cent. Deficient aeration handicaps the deeper-seated roots, and also exerts an unfavorable effect upon the development of the root itself. The saving of irrigation water with the consequent improvement of soil-aeration is further considered in the report for 1916–17.

Clements (1916 : 90) has emphasized the importance of oxygen in wet habitats in which plant remains accumulate so abundantly as to make the access of air difficult. The decomposition is slow and partial, and the water or soil becomes more or less acid. Lack of oxygen seems a very necessary condition, and the possible effect of the acid upon plant growth is complicated by that of deficient aeration. Both, apparently, act together in diminishing the absorptive power of roots, probably in consequence of decreased respiration. So far as succession is concerned, the production of acid in swamps marks a series of stages which dominate for a time, owing to a favorable response to poor aeration. A recent study of the transpiration and growth of plants in aerated bog-water indicates that the acid is a concomitant only and not a cause. The acid is evidently a by-product of decomposition in the absence of oxygen, and deficient aeration is to be regarded as the effective factor. As a consequence, the measurement of the primary reaction in acid habitats must be directed toward the effect upon the oxygen-content, i. e., upon aeration.

Coventry (1917) stated that for practical purposes it may be assumed that the failure of natural regeneration in the deodar is due to the accumulation of humus and other organic substances, which have interfered with the proper aeration and drainage of the soil. In support of this is the well-known fact that deodar shows a distinct liking for ridges and spurs and similar well-drained places. It is usually found on light, well-aerated soils and does not grow in the heavier clay soils. Some of the best natural reproduction takes place on grassy slopes, which had formerly been subjected to fires, and are consequently well-aerated and drained, owing to the absence of humus.

Hesselmann (1917) has shown that in the pine heaths of Sweden operations which increase the soil-air and the organic matter available for energy promote nitrification, and consequently tree-growth. This may be accomplished by the mixture of decaying leaves or wood with the mineral soil, and especially by logging, which works the surface layer into the soil. A marked increase of nitrification has been secured by mixing sod with the soil or by stirring the latter with the hoe.

Howard (1918 : 187) emphasizes the neglect of aeration as a factor in growth, and reviews briefly the work of Hall on the effect of increased aeration on the root development of barley, and that

of Hunter on the relation of soil-texture to aeration, as well as his own work on the effect of potsherds and sand upon aeration and consequent growth. A somewhat fuller account is given of the studies of Russell and Appleyard on the composition of the soil-air, and the relation of irrigation and water-saving to proper aeration and growth is discussed. The importance of air-content as a limiting factor is indicated, and the relation of quality in barley, tobacco, and cotton to aeration suggested.

Hole (1918 : 202) reviews his study of the relation of aeration to the growth of sal seedlings, and gives the experimental evidence to show that soil organisms greatly decrease the oxygen and increase the carbon dioxid in soils which bear no green plants. He deals with the poisonous effect of carbon dioxid in various quantities, and concludes that injury in badly aerated soils is due to an excess of carbon dioxid as well as to the deficiency of oxygen, while admitting that further investigation of this point is needed. He states that soil aeration depends chiefly upon the amount of water and organic matter in the soil, the number and kind of soil organisms, and the rate at which air or water with oxygen in solution penetrates the soil. Finally, he suggests, as Howard has earlier, that the injurious effect of grass on fruit trees may be due to poor aeration.

Howard and Howard (1918 : 36) have described a new method of pit cultures for the study of air and water relations under essentially natural conditions, and have employed it for determining the effect of mixing the Pusa soil with potsherds and sand on the growth of Java indigo. The average length in soil only was 36.7 cm., in equal parts of soil and sand, 51.6 cm., in soil with one-tenth of potsherds, 48.3 cm., and in soil with three-tenths, 50.9 cm., the respective percentages of increase being 40, 31, and 38. Potsherds at the rate of 1 inch per acre increased the yield of oats 18 per cent, wheat 20 per cent, and tobacco 10 per cent. In the case of alfalfa, one-third potsherds gave an increase of 24 per cent, and one-half windblown sand an increase of 42 per cent (1918[2]).

Sen (1918) has shown that the addition of 30 per cent of potsherds to soil greatly increases nitrification. The dissolved oxygen is much greater with 10 to 30 per cent of potsherds than with none, and the oxidation of organic matter is correspondingly hastened. A fall of rain leaches out some of the nitrates and is apt to give rise to denitrification, but the oxygen of the rain-water increases the amount in the soil-air and hence tends to stimulate nitrification. The downward movement of rain, and especially of the water-table, causes greater aeration of the soil, and results in more active nitrification.

Howard and Howard (1919) have given a further account of the effect of water-logging on the development of roots and of the influence of drainage upon crop production, and have summarized the various experiments upon the saving of irrigation water (1919[2]).

In a final paper on indigo wilt (1920), they state that the conclusion is irresistible that the trouble results from the destruction of roots and nodules under conditions in which regeneration is impossible. If floods cause the ground-water to rise, or if heavy rainfall waterlogs the surface soil for long periods, the defective aeration makes root regeneration very difficult, and wilt ensues. In confirmation, it has been shown that other deep-rooted species exhibit wilt, while varieties of these with shallow roots do not. Moreover, wilt is common in years of heavy rainfall, and rare or of slight importance in dry years, while it is seldom found in porous soils.

Clements (1920 : 85) recognizes that plants may serve as indicators of good or bad aeration and has discussed the subject as follows: The effects of wet and acid soils upon plant behavior have long constituted a puzzling problem. The leading rôle in such habitats as marshes and bogs has been assigned to various factors, such as acids, bog-toxins, toxic exudates, the absence of lime, and the lack of oxygen. Probably all of these are more or less concerned in the problem, with the exception of the supposed exudates, but the view held here is that lack of oxygen is the cause, and the other conditions consequences or concomitants (Clements, 1916 : 90). The presence of acids and bog-toxins is regarded as the direct result of the activity of the roots and bog-flora under deficient aeration (*Cf.* Stoklasa and Ernest, 1908 : 55; Livingston, 1918 : 95).

The absence of lime is apparently a concomitant of acid production, since the addition of lime to an acid soil either neutralizes the acid or affects the colloidal relations in such fashion as to make the soil agriculturally productive. It is significant, however, that lime is not the only substance that has this effect, since it is also produced by other materials which improve aeration. An acid soil is regarded as unfavorable to plant-growth primarily because of the deficit in oxygen, and consequently also because of the poor development of the micro-organisms that reconvert organic nitrogen into available form. The current assumption that bog-water contains acids or toxins which are in themselves unfavorable to absorption seems disproved by the experiments of Bergman.

Plants may indicate good or bad aeration. The former are naturally of little importance as aeration indicators, since their impress is due to some other factor or factor-complex. Aeration indicators proper are correlated with a deficiency of soil-oxygen, and are naturally confined to wet soils and water, owing to the inverse relation existing between the amount of water and of oxygen. They may be conveniently arranged in four groups, based upon the kind of response to deficient aeration. In the first two the species have developed adaptations which enable them to live so successfully in swamps and bogs that the habit is now obligate for the majority of them. The species of swamps regularly possess a special aerating

system of air-passages and diaphragms, often supplemented by superficial roots and a marked movement of the transpiration stream. Such indicators are found typically in *Equisetum, Juncus, Heleocharis, Scirpus, Alisma, Sagittaria, Sparganium,* etc. Air-passages also occur in some bog-plants, but they are little or not at all developed in the shrubby species, such as *Vaccinium, Ledum, Andromeda, Kalmia, Empetrum,* etc. In most of these the aeration devices are subordinate to those designed to conserve the water-supply during drought, especially in winter (Gates, 1914). Coville (1911, 1913) has emphasized the importance of good aeration for the successful culture of the blueberry, pointing out that this is secured in nature by the superficial roots as well as by their position in hummocks. It is probable also that mycorrhiza plays an important rôle, partly in increasing the available nitrogen, and partly also perhaps in directly compensating for the deficit in oxygen.

The other two groups of aeration indicators consist of plants which grow normally in well-aerated soil. Hence they lack special adaptations for aeration and consequently serve to indicate a lack of oxygen by their growth or distribution. Those which are somewhat tolerant of water-logged and poorly aerated soils respond to reduced oxygen-content by decreased growth and reproduction. Intolerant species drop out, and their reduced number or absence serves as an indicator of conditions.

Summary.—The results of field studies of aeration are in complete agreement with those obtained from physiological investigations as to the basic importance of oxygen for root activity and the injury wrought by the accumulation of carbon dioxid. The detailed significance of the lack of oxygen and the abundance of carbon dioxid as ecological factors is discussed in connection with bog xerophytes and soil toxins. Here it will suffice to point out that field research has approached the problem of an oxygen deficit from four different angles, and that the results and conclusions are all in essential accord. The agricultural approach has been made by Sorauer, Dehérain, Wollny, Brizi, Ehrenberg, Balls, Harrison and Aiyer, Howard and Howard, Main, and Allan, and that of forestry by Vonhausen, Böhm, Mangin, Hesselmann, Bernbeck, Hole, Hole and Singh, and Coventry. Pathological considerations have entered into many of the studies, but they have received especial attention at the hands of Sorauer, Hartig, Mangin, Howard, and Graves, while the ecological outlook has been represented by Warming and Clements. Moreover, a large number of the papers in the next two sections have a more or less direct bearing upon the ecological and practical significance of aeration, but are discussed later, owing to their relevance to the special problems concerned.

The inverse relation of water and soil-air is chiefly discussed in the following sections, but the significance of irrigation-water in this connection has been largely determined by Howard and Howard in their investigations of aeration as a primary factor in agriculture.

Widtsoe (1914 : 249) has probably been the first to show that there is a steady decrease in the yield of wheat per inch of water as the irrigation of a field is increased, and that excessive irrigation may produce an actual decrease in the total yield, though he did not recognize that this was chiefly due to faulty aeration. The rapid decrease in production for each inch of water used is shown in table 27.

Two irrigations amounting to 7.5 inches are regarded as sufficient for a crop of wheat on deep soil, and 4 to 5 irrigations, totaling 18 inches, on shallow gravelly soil. On many soils a single irrigation of 5 inches is better.

TABLE 27.

Inches of water applied.	Bushels of wheat for each inch.	Bushels of grain to the acre.
5.0	7.56	37.81
7.5	6.39	41.54
10.0	4.35	43.53
15.0	3.05	45.71
25.0	1.86	46.46
35.0	1.39	48.55
50.0	0.99	49.38

Howard and Howard (1915, 1919) have published two bulletins on the saving of irrigation-water in wheat-growing, which deal with the principles underlying water-saving, and with experiments at Quetta and in India. The six principles are the following:

(1) The irrigation-water available should be spread over the largest possible area.

(2) Irrigation-water must be applied in such a manner as to interfere as little as possible with the natural aeration of the soil.

(3) Heavy waterings reduce the proportion of grain to total crop.

(4) The growth-period of wheat is increased by heavy watering.

(5) When the water-supply is limited, the root development of the wheat crop must be deep.

(6) The soil-moisture must be preserved as far as possible by a surface mulch of dry soil.

While all of these relate to aeration as well as water economy, the first three have to do directly with a proper supply of soil-air. Other things being equal, the soil-air is increased as the irrigation-water is diminished, and with respect to the plant alone, the best irrigation method involves the most effective compromise between too much water and too little air (table 28).

The economic waste involved in using irrigation-water beyond the optimum is threefold. The most serious waste occurs when an actual reduction of the yield per acre takes place, but scarcely less important is the waste resulting from a rapidly diminishing return per acre-inch of water used. In average seasons such waste amounts at least to much of the cost of the water, and may amount to the

value of the crop that could be produced with the superfluous water, while in seasons of drought it may often reach the total value of the average crop. In the third place, excessive irrigation works injury to the fertility of the soil, largely as a matter of defective aeration. Thus, Main (1916 : 47) has shown that continuous cropping to wheat with several irrigations has reduced the yield per acre at Mirpurkhas from 759 pounds in 1908–09 to 372 pounds in 1913–14, in spite of the use of fertilizers.

TABLE 28.—*Water-saving experiments on wheat, 1916–17.*

QUETTA.

No. of waterings.	Area.	Total weight of produce.	Total weight of grain.	Yield of grain per acre.	Reduction.
	acres.	*lbs.*	*m. s.*	*m. s.*	*p. ct.*
1	3.99	10,367	52 6	13 2	0
3	2.65	6,620	25 15	9 23	26

GUNGAPUR, HARIPUR, AND SARGODHA.

Total No. of irrigations.	Yield per acre.				Average yield per acre.			
	Grain.		Straw.		Grain.		Straw.	
	m.	*s.*	*m.*	*s.*	*m.*	*s.*	*m.*	*s.*
1	12	19	20	10	..	..	..	..
1	8	31	19	14	9	34	21	17
1	8	12	25	27	..	..	..	..
2	18	..	25	8	..	..	..	..
2	15	21	23	16	16	11	25	5
2	15	12	26	32	..	..	..	..
3	14	25	18	..	..	..	..	..
3	16	8	26	4	15	11	22	2

NOTE.—In Mirpukhas one watering yielded 1,483 pounds, two yielded 1,471.

It appears almost certain that the common practice in irrigated regions involves the use of too much water, with the consequent economic losses. Not the least of these is the necessary restriction of irrigation systems to a smaller territory than should be the case, which results in a serious limitation of opportunity and production. Throughout the western United States it is a fortunate system that does not face an annual or periodic deficit, while the extent of new reclamation projects must unfortunately be determined by the existing practice rather than by the optimum duty of water. As a consequence, it would seem an indispensable task of every great system, installed or to be installed, to determine the optimum use of water and to take steps to see that everyday practice conforms to the findings. Moreover, while annual crops quickly show the effect of

over-irrigation and defective aeration, perennial and especially woody plants exhibit damage less readily, with the result that they often gradually develop diseases obscure in origin and impossible of reference to a specific parasite as a cause. In all such cases it is necessary to consider as a possible cause the defective aeration that regularly arises as a consequence of applying too much water. In older districts the gradual rise of the water-table brings in its train the evils of an oxygen deficit in the soil, and this must frequently be the real cause of the troubles that are often referred to the presence of alkali.

II. BOG XEROPHYTES AND ACID SOILS.

The true nature of bog and swamp plants that possess apparent xerophytic structures has been a subject of discussion since Volkens and Zingeler first observed the protected stomata of many hydrophytic species of *Carex*. The concept of bog xerophytes was definitized by Warming (1895) and by Schimper (1898), the latter regarding them as outstanding examples of physiological drought. This interpretation was first questioned by Clements (1905, 1907), who showed that the transpiration and growth of certain so-called bog xerophytes were those of hydrophytes. Since this time a number of studies have dealt with this problem (Yapp, 1909; Sampson and Allen, 1909; Gates, 1914; Folsom, 1918; Dosdall, 1919; Bergman, 1920; Clements and Goldsmith, 1921), with the result that the number of supposed bog xerophytes has steadily decreased. In the series of investigations under way it is hoped to make a comparative study of the water-relations of the majority of bog and swamp plants that have been regarded as xerophytes, and consequently to ascertain the real significance of their xeromorphic characters.

THE NATURE OF BOG XEROPHYTES.

Earlier views.—The first observations on the discrepancy between structure and habitat were made by Volkens (1884 : 23; cf. Zingeler, 1873 : 127). It was found that certain species of *Carex*, e. g., *C. glauca*, *gracilis*, *limosa*, *maxima*, *panicea*, and *paniculata*, possessed stomata with papilliform projections that extended from the accessory cells over the openings, forming a chamber protected from dry air. Volkens stated that from all the analogies this adaptation must serve as a device against excessive transpiration, and yet it was characteristic of species without exception that thrive only in wet soil. Moreover, this protective device was found to be absent in the species of dry soil. He sought to explain why sedges growing in wet soil should reduce water-loss by covering the stomata by the fact that the ground-water sank in midsummer, thus causing a certain amount of drought in the upper layers.

Warming (1888 : 125) showed that several swamp species of *Carex* exhibited the same structure of the leaf as that found in pronounced heath-plants, such as *Carex nardina* and *Elyna bellardi*. As a consequence of the lack of harmony with the habitat, he was inclined to regard the structure of the leaves as the common heritage of the group *Monostachyæ*, which was independent of the habitat.

From a study of the stomata of certain grasses and sedges Schwendener (1889 : 76) concluded that the structural characters which are

to be regarded as adaptations to conditions without exception among the endemic species of *Carex* do not always correspond to the present habitats in the case of the derived ones. The steppe characteristics shown by some grasses and grass-like plants of the flora have plainly arisen in response to the great climatic extremes of their original home, and not out of their present habitats in Germany. He regarded it as probable that this conclusion held also for the ericoid leaf-forms, waxy coating, scale-hairs, and similar adaptations which reduce transpiration and in particular protect the stomatal openings and are apparently lacking among endemic plants.

In contrast to the views of Warming and Schwendener, Kihlmann (1890:80, 105) sought the explanation of the protective devices of bog-plants in the factors of the habitat. He cited the opinion of Hartig (1880), who emphasized the similarity between the effects of winter-killing and those of drying-out arising from a lack of water, and stated that very many cases of winter-killing are really due to the drying of leaves and shoots at a time when the absorption of water from the frozen soil is impossible. He also repeated and confirmed Sachs's results with plants whose roots were surrounded with ice, finding that they wilted quickly and completely in the sun, while control plants suffered not at all. Consequently, transpiration was regarded as the most important factor in retarding tree-growth in the north. It is not the mechanical force of the wind itself, the cold, the salt-content, or the humidity that sets a limit to the forest, but chiefly the uninterrupted drying-out of the young shoots at the time of the year when replacement of the water transpired is impossible.

While Kihlmann recognized the significance of the dry climate of polar regions, and especially of the low humidity of the air, as emphasized by Warming and others, he regarded the latter as not sufficiently low in summer to alone explain the phenomena. In his opinion, a more potent factor was the sudden and marked lowering of the temperature of soil and air through the entire growing-period by a sudden fall of snow or by an icy rain, while the strong winds maintained transpiration at an active rate. The relatively small snowfall in winter and its unequal distribution explain why the drying-out of the plant-cover over wide stretches continues as in summer and to an unusual degree. Consequently, the slightest difference in level can produce a sharp difference in vegetation. The moisture of the underground ice is but slightly available, as a result of the very slow melting in summer, and it can not protect the plants from drying-out if they are not able to absorb and use the ice-cold water. As a consequence, it is readily understood why so many arctic plants, and among them the most universal and widely distributed, show a marked adaptation to drought, and especially to dry air.

Transpiration is dependent not only upon insolation, air-temperture, and relative humidity, but also upon the strength of the wind, while root activity is determined chiefly by soil-temperature. The open swamps and morasses of polar regions are at once the windiest and possess the coldest soils of all habitats on the earth's surface. The temperature of the soil remains very low for a long time after snow has disappeared, owing to the gradual melting of the subterranean ice, and even in midsummer the uppermost layers of the wet soil are almost always constantly and considerably colder than in the drier habitats. Even while the root-system is still partially frozen at least, some species, such as *Eriophorum vaginatum*, begin to form shoots and leaves, often to expose them for a long time to the drying breath of the polar winds. In spite of excessive water-content and relatively high humidity, swamp-plants are thus exposed to severe drying-out, and many of them require protection against this danger.

It is a well-known fact that in the high north many true swamp-plants, such as *Ledum*, *Betula nana*, *Andromeda*, and *Myrtillus uliginosa*, grow also in dry, sunny habitats, which without doubt must frequently be very dry. Further south, *Calluna* and *Empetrum* exhibit a similar behavior, in that they grow in high moors and at the same time in a dry, sandy soil, where the transpiration is much greater. The explanation of this lies in the fact that the evergreen shrubs of the swamp are annually exposed for a considerable time to marked water-loss, when the ground is frozen and the snow insufficient to protect them. The great majority of the plants of peat-moors and swamps are therefore of a type that can withstand drying-out in the air and must often be exposed to it. In some the leaves are scale-like or needle-like, stiff, and strongly cutinized (*Lycopodium*, *Diapensia*, *Andromeda hypnoides*), or they tend to be succulent (*Saxifragra oppositifolia*, *Eutrema*, *Rhodiola*). The stomata are sunken or inclosed in hollows (*Andromeda tetragona*, *Empetrum*) or covered with a dense layer of hairs below (*Ledum*, *Dryas octopetala*, *Potentilla nivea*, *P. multifida*, *Loiseleuria procumbens*, *Phyllodoce*). In other cases, the stomatal lower surface is covered with a thick coating of wax (*Andromeda polifolia*, *Vaccinium vitis-idœa*, *Salix glauca*, and *S. reticulata*). Among the grass-like plants are a large number of northern species that must be placed in the steppe type by virtue of the rolling, hardness, and strong cutinization of the leaves (*Hierochloe alpina*, *Festuca ovina*, *Nardus*, *Carex rupestris*, *C. pedata*). In addition, there are many other sedges and rushes of xerophytic appearance, such as *Scirpus cæspitosus*, *Carex diœca*, *chordorrhiza*, *limosa*, *parallela*, *pauciflora*, *Juncus biglumis*, *triglumis*, and *filiformis*, as well as *Equisetum fluviatile*. It can not be denied that some swamp-plants have no devices for reducing transpiration. These are species with soft leaves, which neverthe-

less do not avoid the windiest and most unfavorable habitats. The most notable are *Rubus chamæmorus, Pedicularis lapponica, Nardosmia frigida, Ranunculus pallasii,* and, even more sensitive, *Hippuris, Caltha, Epilobium palustre* and *davuricum, Cardamine pratensis, Comarum,* etc. Their specific property seems to be a raising of the functional ability of the tissue to a maximum of resistance against cold.

Schimper (1890) stated that devices which indicate inadequate water relations occur among plants of many habitats, where they can be explained neither through low water-content nor inheritance. His researches showed that in all cases where protective devices against transpiration were found in the structure of plants a need for such protection actually existed, but that this might be brought about by very different causes. For example, such protective devices are quite common in the case of halophytes, alpine plants, and evergreen woody plants of the north temperate zone. Protection against transpiration is necessary for halophytes on account of the greater difficulty of absorption resulting from the high salt-content, and because concentrated solutions of salt hinder photosynthesis, while still more concentrated ones result in the death of the organs. The alpine flora of Java owes its highly peculiar impress not to low temperatures, but to protective devices against transpiration. It is clear that the rarefication of the air, together with its direct influence upon transpiration and the indirect influence of the stronger insolation, is to be regarded as the most important cause of timberline and of the xerophyll character of these tropic alpine formations. The flora of the solfataras has a pronounced xerophytic character, and there can be no doubt that here, as in the case of the mangrove, the chemical nature of the substratum makes protective devices against transpiration a necessary condition of life. The retarding effect of a lower temperature of the soil upon the water absorption of the plant makes it also conceivable why alpine plants that grow in melted snow, like *Ranunculus glacialis,* or on glacial streams, like *Saxifraga aizoides,* exposed to the glowing rays of the alpine sun, are thick-leaved or succulent, like the inhabitants of dry habitats. Moreover, the peculiarities of polar plants, which show so many analogies with those of deserts, may be related to similar causes. Biologically all these peculiarities are wholly intelligible, and it is only necessary to advance proof that such protective devices occur in all plants which permanently or periodically have to contend against a lack of water, whether the cause is to be sought in dryness of the air and soil, in stronger insolation and rarefication of the air, in the salt-content of the soil, or in the lower temperature of the latter.

Goebel (1891 : 11) investigated the discrepancy between habitat and adaptation in the vegetation of the Paramos of Venezuela. The greater humidity was regarded as causing the greater luxuriance in

vegetation of the Paramos in contrast with that of the Punas. This is all the more striking, since the vegetation of the first has in the main an evident xerophilous character. This is due not only to the amount of soil-water, but also to other conditions. Sachs has shown long ago that the absorption of water from the soil was related to the presence of a proper temperature. Plants can wilt in a soil rich in water if the absorption of the roots on account of the low temperature is less than the water-loss. In the Paramos the cooling-off of the soil is significant and the change in temperature rapid, while the warming-up through the sun lasts only a short time and is of little effect in the wet spots. About 11 o'clock the Paramos are usually shrouded in cloud and fog, and the sun indeed is often hidden before this time. The roots, as a consequence, grow in a soil almost always cold, and the absorption of water is relatively small. On the other hand, transpiration is increased by the strong winds and the rarefied air. These factors work together to explain the peculiar fact that xerophilous vegetation occurs in habitats that are rather to be called wet than dry. Thus, the thick woolly *Espeletia* and *Culcitium* were not rarely found in the middle of swamps. Meigen (1894) supported the views of Kihlmann and Goebel as to the causes of the xerophytic characters of swamp plants.

Warming (1895, 1896, 1909 : 193) enumerated the following swamp species which exhibit xeromorphy to the extent that they are protected by certain devices from desiccation:

Hairy coating:
Ledum grœnlandicum.
palustre.
Salix glauca.
lanata.
Cassandra calyculata.
Nyssa uniflora.
Persea pubescens.
Magnolia virginiana.
Stomatal papillæ:
Carex limosa.
panicea.
rariflora.
Lysimachia thyrsiflora.
Polygonum amphibium.
Waxy coating:
Vaccinium uliginosum.
Andromeda polifolia.
Vaccinium oxycoccus.
Salix grœnlandica.
Acer rubrum.
Persea pubescens.
Waxy coating—con.:
Carex panicea.
Primula farinosa.
Thick cuticle:
Scirpus.
Leathery leaves:
Andromeda polifolia.
Vaccinium oxycoccus.
vitis-idæa.
Ledum palustre.
Mucilage:
Berchemia scandens.
Pieris nitida.
Ericoid leaves:
Erica tetralix.
Calluna vulgaris.
Empetrum nigrum.
Juncoid leaves and stems:
Equisetum limosum.
Junci genuini.
Scirpus cæspitosus.
lacustris.
palustris.
Juncoid leaves and stems—con.:
Eriophorum vaginatum.
Carex microglochin.
dicœca.
chordorrhiza.
pauciflora.
Erect or equitant leaves:
Iris.
Narthecium.
Acorus.
Xyris.
Alisma plantago.
Sagittaria latifolia.
Butomus.
Typha.
Sparganium.
Ranunculus lingua.
Lathyrus nissolia.
Closure of leaves:
Carex goodenowii.

Warming regards it as evident that there must be a causal connection between the soil and the xeromorphic structures, i. e., the soil must be physiologically dry, and hence some of the conditions under which marsh-plants live compel them to conserve water. The various factors thought to be concerned and often to cooperate are:

(1) a transpiration optimum; (2) physiological dryness in wet, cold soil; (3) poor soil-aeration; (4) water-retention in peat soil; (5) chemical substances; (6) free humous acids and other dissolved substances that chemically affect the roots and are regarded as the chief cause of physiological dryness. These are thought to depress the root's acitivity and consequent absorption. Warming, however, also recognizes the presence of hydrophytes in moors, which are not in harmony with the supposed dryness of the habitat, such as *Rubus chamæmorus*, *Caltha palustris*, and *Viola palustris*.

Stenström (1895 : 117) discussed in an exhaustive fashion the relation of species to different climates and habitats, and reached the conclusion that Kihlmann's explanation of bog xerophytes was not true. He cited Burgerstein's results with humus extract to support the view that such substances explain the xerophily of bog-plants. His explanation of the latter was based chiefly upon the transpiration relation and the fixity of inherited structures. His views upon transpiration seem to be unsound, and he himself admitted the paradox involved in them (p. 184), stating further that the effects supposed to be due to transpiration might well be caused by poor aeration. As to the origin of unplastic or stable plants, such as *Ledum palustre* and *Pirola rotundifolia*, he pointed out that they were probably of great age phylogenetically, and that the evergreen character had persisted under widely different conditions, since the period of tropical climates in high altitudes.

Schimper (1898, 1903) broadened the concept of non-available water, and emphasized the distinction between physical drought, in which the soil itself is dry, and physiological drought, where the soil is wet but much of the water not available to the roots. He mentioned soils rich in humous acids and those with temperatures at or near freezing as examples of physiological dryness, which led to xerophytic vegetation in such habitats. He also stated that many plants that thrive in meadow-moors were completely absent from high moors, apparently kept away by the great amounts of humous salts in solution. The presence of xerophytes in swamps and bogs was explained by the occurrence of humous acids, which hindered the absorption of water by the roots and rendered the soil dry to plants, and hence well-suited to xerophytes. Nothing is said as to why humous acids have this effect, but it is possible that the assumption was based upon a mistaken statement in Pfeffer's Physiology (1897, 1:231; 1900, 1:249), to the effect that "transpiration is *decreased* by the addition of small quantities of tartaric, oxalic, nitric, or carbonic acid to the soil, whereas it is *increased* by alkalies, such as potash, soda, or ammonia, as Sachs has shown and Burgerstein has since established more in detail."

Later views.—Früh and Schröter (1904 : 14) stated that the controlling factors in low moor and high moor were the water-retaining power of the peat, the low temperature, and the lack of oxygen, which hindered the respiration of the roots and consequently all their functions. These conditions make the absorption of water difficult, producing the physiologically dry soil of Schimper. The xerophytic character of many species of the low moor, as shown in the terete leaves of *Cyperaceæ* and *Juncaceæ*, stomatal protection and roll-leaves in *Carex* and *Poaceæ*, equitant leaves in *Iris* and *Tofieldia*, waxy coating in *Primula farinosa*, small leaves in *Lysimachia*, *Epilobium*, *Veronica*, and *Centaurea*, and marked cutinization in *Scirpus*, are not entirely clear in their significance. They bear some relation to the greater difficulty of absorption, but probably in spite of this the higher water-balance is made possible through the inability of all of these plants to close their stomata. Similar xerophytic characters in the high moor, such as the ericoid leaf of *Calluna*, *Empetrum*, and *Oxycoccus*, the leathery leaf of species of *Vaccinium*, etc., are due partly to the more difficult absorption of water and partly to the evergreen nature of these plants. Many typical inhabitants of high moors can grow likewise in habitats very dry physically, but most of the species of low moor are strict hydrophytes and do not thrive in dry soil.

Clements (1905 : 126; 1907 : 169) first questioned the conclusion of Schimper that bog xerophytes are due to the presence of humic acids which inhibit absorption and aeration in the roots, and that bogs and swamps are consequently physiologically dry. The fact that weak solutions of organic acids usually increase transpiration was regarded as making it improbable that small quantities of humic acids should decrease absorption sufficiently to produce xerophytes in ponds and bogs. Moreover, not a trace of acid was discovered in many ponds and streams where *Heleocharis*, *Scirpus*, *Juncus*, etc., grow. Plants with a characteristic hydrophytic structure throughout are regularly found alongside of apparent xerophytes, and these also show a striking contrast in size and vigor of growth where they grow both upon dry gravel-banks and in the water, indicating that the available water is much greater in the latter. The conclusion was reached that the xerophytic features found in amphibious plants are due to the persistence of stable structures, which were developed when these plants were growing in xerophytic situations.

Clements grew *Ranunculus sceleratus* (1905 : 120, 156) and *Sagittaria latifolia* (1907 : 169) in various water-contents under control, and found that the amphibious form in swamps was a hydrophyte, as shown by the differences between it and artificially produced xerophytic forms, in growth, number of stomata, and transpiration. Folsom (1918 : 809) has later grown *Ranunculus sceleratus* under control with similar results.

Sampson and Allen (1909 : 49) studied the transpiration of *Scirpus lacustris* in comparison with that of *Helianthus annuus*, a pronounced mesophyte, and found that the former lost water almost twice as rapidly. Dosdall (1919 : 35) has shown that the transpiration of *Equisetum fluviatile* is twice that of *Helianthus annuus*, and Clements and Goldsmith (1921) have recently found that *Typha* transpires several times as rapidly as the sunflower.

Transeau (1905 : 17) has studied the structure of a number of representative bog-plants or bog-forms, namely, *Eriophorum virginicum*, *Sarracenia purpurea*, *Oxycoccus macrocarpus*, *Andromeda polifolia*, *Chamædaphne calyculata*, *Chiogenes hispidula*, *Vaccinium corymbosum*, *Salix sericea*, *Ledum grœnlandicum*, *Larix laricina*, *Picea mariana*, and *Pinus strobus*. In general, they are characterized by a thick cuticle, waxy coatings and hairs, thick-walled epidermal and hypodermal tissue, the presence of palisade tissue, and of resinous bodies in the roots and leaves. There is a general reduction in the size of the leaves, which are often revolute, and mycorrhizal fungi are present in the roots of most. They resemble the xerophytes of dry sandy plains in the reduced leaves, epidermal characters, and palisade tissue, but differ greatly in root development and structure. All of the woody plants listed possessed mycorrhiza, with the exception of *Andromeda*, *Chamædaphne*, and *Salix*, and it was observed likewise in *Betula lutea*, *B. pumila*, *Oxycoccus oxycoccus*, and *Populus tremuloides*. In the case of *Larix*, it was found that mycorrhiza developed only in poorly aerated substrata and that plants formed normal roots under aeration, or in a soil naturally well-aerated. It was concluded that acidity had nothing to do with the production of mycorrhiza, since normal roots were developed in acid water-cultures.

Yapp (1909 : 309) has shown that there is a marked difference in the evaporation at different levels in a marsh community. In vegetation 5 feet high, the evaporation was 100 just above, 32.8 in the middle, and 6.6 at the soil level, while in that 2 feet high it was 100 just above, 56.2 just below, and 14.7 at the bottom. He concludes that the mutual protection from excessive transpiration and the mechanical effects of the wind, derived from the grouping of shoots, is probably beneficial, even apart from the more obvious cases where the climate is exceptionally rigorous. The structural features of vegetation may thus be effectual in securing immunity from excessive transpiration. Different species vary as to the depth of the root-system, height of shoots, relative position of transpiring surface, and length of vegetative period. Few of the species in a swamp-moor live under precisely the same set of physical conditions. Thus, the arguments of authors, who insist that the so-called xerophytic structures of marsh-plants are not due to present-day conditions, because both xerophytes and non-xerophytes often grow side by side, are entirely inconclusive. However, this last statement would doubtless have

been much modified if the author had determined the transpiration at the different levels, since it is almost certain that this would have shown *Phragmites* and *Cladium* to be hydrophytic in both transpiration and stomatal behavior, as *Scirpus* and *Typha* are known to be.

Coville (1910) has demonstrated that the swamp blueberry (*Vaccinium corymbosum*) requires a well-aerated soil for active growth and can not grow readily in soil saturated with water. Sandy soil and drained fibrous peat offer satisfactory conditions, as well as live moist sphagnum hummocks, which furnish permanent moisture and thorough aeration. The rootlets of the blueberry contain an endotrophic mycorrhiza, probably belonging to the genus *Phoma*. It is assumed as possible that this is able to assimilate atmospheric nitrogen much more actively than *Clostridium*, and also that it makes the non-available nitrogen of the peaty soil available to the plant, thus making up for the great lack of available nitrates, due to the inability of nitrifying bacteria to thrive in the acid soil. The swamp blueberry grows in peaty soils that contain acids or other toxic substances and suppresses the root-hairs as a protection against these. As a consequence, both absorption and transpiration are low, and many bog shrubs show devices for retarding water-loss similar to those of desert plants. Low absorption leads to insufficient nutrition, and the danger of nitrogen starvation is especially great, owing to the lack of nitrates. In the swamp blueberry the necessary nitrogen is secured by means of the mycorrhizal fungus, and conveyed into the plant without a large amount of the poisonous water.

Burns (1911 : 124) concluded that the bogs around Ann Arbor contain xerophytic, hydrophytic, and even mesophytic areas. The presence of definite communities in each zone is due chiefly to soil conditions, especially temperature, and also to the position of the water-table and to aeration. Of the 7 zones described, but 3, the floating sedge, bog shrub, and tamarack, have dominants that are xerophytic in nature. In the sedge community only the plants that root deep in the floating mat are regarded as box xerophytes, while those rooting in the surface are hydrophytes. The chief mat-forming plants are *Carex filiformis* and *C. oligosperma*. Associated with these, some playing an important part in mat formation, are *Menyanthes trifoliata, Dulichium arundinaceum, Eriophorum viridi-carinatum, Drosera rotundifolia, Aspidium thelypteris, Onoclea sensibilis, Equisetum limosum, Eupatorium purpureum, E. perfoliatum, Mentha arvensis glabrata, Scutellaria galericulata, Utricularia, Calopogon pulchellus, Campanula aparinoides, Arethusa bulbosa, Galium trifidum, Aster junceus, Potentilla palustris, Solidago serotina, Lysimachia terrestris*, etc. The characteristic plants of the bog-shrub zone include *Chamædaphne calyculata, Andromeda polifolia, Betula pumila, Nemopanthes mucronata, Sarracenia purpurea, Vaccinium oxycoccus, V. macrocarpum*. The principal plants of the tamarack zone are

Larix laricina, Cornus stolonifera, Osmunda regalis, O. cinnamomea, Rhus vernix, and *Aster junceus.*

Rayner (1913, 1915) has shown that when seeds of *Calluna vulgaris* are sterilized and germinated in sterile conditions, root-growth is retarded and finally inhibited in the absence of mycorrhizal infection. Pot cultures in soils favorable and unfavorable to the growth of the plant in the field demonstrated that *Calluna* grew normally in the one and abnormally in the other, as indicated by poor germination, the stopping of growth in root and shoot, and the presence of bacterial colonies on the roots about the tips. The relation between the plant and its mycorrhiza seems to be obligate, and normal growth is dependent upon early infection and the healthy growth of the fungus. The usual preference for an acid soil is explained by the fact that lime prevents the normal development of the fungus and promotes the growth of the colonies of bacteria, interfering with the symbiotic relations of the root and its proper functioning. Further studies of the fungus showed that it is not confined to the roots, but is found also in stems, leaf, flower, and fruit. Seedlings free from infection did not form roots, but underwent complete cessation of growth, remaining alive but rootless for months. It is regarded as possible that the presence of the fungus in stem and leaf permits it to fix atmospheric nitrogen.

Gates (1914 : 472) has shown that the summer transpiration of *Chamædaphne* is much less than that of such hydrophytes as *Sagittaria latifolia* and *Carex filiformis,* while *Andromeda* transpires nearly as much as *Potentilla palustris* and somewhat more than *Aspidium thelypteris.* The rate of conduction in the evergreen heaths was found to be much lower than that of the hydrophytes. The latter exhibited the highest rate of water-loss per unit area, and in general herbs transpired more rapidly than shrubs. The more hydrophytic swamp-shrubs transpired more vigorously than the typical bog-shrubs, and the deciduous more than the evergreen. Water-loss in the deciduous *Larix laricina* was noticeably greater than in the deciduous broad-leaved *Acer rubrum,* and decidedly higher than for the evergreen conifer, *Picea mariana.* The transpiration of the evergreen shrubs was several to many times greater than that of the deciduous shrubs during the winter, under both outdoor and indoor conditions. The author states that some so-called xerophytic plants use as much or more water than ordinary mesophytic plants, but they are xerophytic because they can not absorb a large amount of water in proportion to that which they would otherwise transpire. This is puzzling, and is in opposition to the later statement that the determination of the rate of transpiration per unit area of leaf-surface by weighing is a satisfactory approach to a knowledge of the demands of plants for water.

Otis (1914 : 478) has determined the transpiration-rate of several reed-swamp dominants and subdominants, namely, *Pontederia cordata*, *Typha latifolia*, *Sagittaria latifolia*, *Scirpus validus*, and *Scirpus americanus*, in comparison with that of the water-lily, *Castalia odorata* and a free water-surface. The highest rate was shown by *Scirpus* and the lowest by *Sagittaria*. The maximum for one day in cubic centimeters per square decimeter was as follows: *Sagittaria*, 1.05; *Pontederia*, 1.812; *Typha*, 2.129; *Castalia*, 2.28; free water, 2.281; *Scirpus americanus*, 3.198; *S. validus*, 3.690. It is significant of the relation of the transpiring surface to the incident rays that the water-lily and free water gave the maximum on the same day, the two rushes on another day, and the three species with erect or ascending leaves on still another day.

Dosdall (1919 : 29) has made a comprehensive study of the water-relations of *Equisetum*, dealing with its transpiration, growth, echard, etc. It was found that *Equisetum fluviatile* wilted at a water-content of 25 per cent, *Ranunculus sceleratus* at 13 per cent, *Helianthus annuus* at 5.6 per cent, and *Equisetum hiemale* at 5 per cent. Experiments with both plants in the same pot showed that *Equisetum fluviatile* wilted in from 2 to 7 days in contrast to 10 to 12 days for *Helianthus*, and 2 to 12 days in contrast to 17 to 19 for *Phaseolus*. *Equisetum arvense* wilted in 5 days, while *Helianthus* required 12 days. The transpiration-rate of *Equisetum fluviatile* was 25 per cent greater than that of the hydrophytic *Ranunculus sceleratus*, about twice as great as that of *Helianthus*, thrice higher than that of *Phaseolus*, and 10 times as great as in the xerophytic *Bryophyllum calycinum*. The water-loss of *E. hiemale* was slightly greater than that of *Helianthus* and much greater than in *Phaseolus*, while in *E. arvense* it about equaled that of the latter. All three species of *Equisetum* guttated vigorously in the greenhouse at night, as well as when placed under bell-jars, showing that the roots have marked powers of absorption. The growth of *Equisetum fluviatile* was much better in mud or when submerged than in a water-content of 35 per cent, branches failing to develop well in the latter, and its water-loss was also much higher in mud. The stomata of both *E. fluviatile* and *E. hiemale* were found to be constantly open, as in hydrophytes generally, and they were more than three times as numerous in the more hydrophytic *E. fluviatile*. The author concludes that the latter is a true hydrophyte, its xerophily being only superficial and probably due to the persistence of ancestral characters, while *Equisetum hiemale* and *arvense* are more mesophytic in their tendencies.

The comparative water-relations of conifers are hardly sufficiently known as yet to make their behavior in bogs entirely clear, but it seems probable that species of *Picea*, *Abies*, and *Pinus* readily withstand the low soil-temperatures found there in consequence of a

xerophily originally produced by winter cold. Several investigators have shown that *Larix* has a higher transpiration than many broad-leaved deciduous trees, and it is practically certain that it is not a xerophyte at all.

Stopes (1907 : 48) has stated that the histological structure of gymnosperms is incapable of allowing a rapid flow of water through the wood, and hence the plants must set strict limits to leaf-surface and transpiration. Even though growing with leafy deciduous trees in a mesophytic community well supplied with water, the conduction of the latter through the woody stem is insufficient for anything but xerophytic foliage. Consequently, the xerophytic characters of conifers are regarded in very many cases as not adaptations to xerophytic conditions at present, or as inherited from the remote past as vestigial characters, but as the result of physiological limitations of the type of wood. A comparative study of transpiration in conifers and deciduous trees in various habitats and altitudes is now under way at the Alpine Laboratory, and it is hoped that this will throw new light upon the nature and causes of xerophytism in conifers.

Groom (1910 : 251) concluded that the xerophytism of conifers was partly architectural in nature, as shown by the fact that the aggregate leaf-surface of the conifer is often much greater than that of the dicotyl tree, although the individual leaf is small. Despite the low rate of transpiration for a single leaf or a unit of its surface, at least some north-temperate conifers expend and need as much water as do some dicotylous trees. The aggregate leaf-surface of cold-temperate conifers is such that even their xeromorphic and xerophytic leaves do not prevent numbers of species from succumbing from desiccation or growing feebly in places where ordinary dicotyl trees thrive. Such conifers are architectural xerophytes in which the extensive aggregate surface of the tree makes it necessary for the individual leaves to be xeromorphic in form and xerophytic in structure. This enables them to live in regions where there is a season of physiological drought in situations varying from dry dunes to moist forests and from arctic and alpine situations to tropical sites. The tracheidal nature of their wood is not a bar to progress and the adoption of the deciduous habit, for in the larch a rapid transpiration current flows through it and the leaves transpire rapidly. In spite of the author's conclusions, however, conifers seem to be chiefly winter xerophytes, and the great increase of total surface for adequate photosynthesis in summer.

According to von Höhnel, the trees transpired as follows in grams of water per unit of air-dry leaf-weight from April 1 to September 31, 1879: Larch, 1,150; linden, 1,030; beech, 860; birch, 845; elm, 755; oak, 660; maple, 520; spruce, 210; Scotch pine, 105; Austrian pine, 100; fir, 75. In rate of movement in the stem, Groom found rates of 204, 233, 240 cm. per hour in the larch in contrast to a maximum

of 232 for beech. As to leaf-surface and water-loss, von Höhnel's results were as given in table 29.

TABLE 29.

Tree.	Aggregate surface in sq. cm.	Water lost June 1 to Sept. 1, grams per sq. cm.
Picea excelsa.....	14,256	0.13
Pinus silvestris ...	5,323	0.17
Abies pectinata ...	12,394	0.18
Acer platanoides ..	4,435	0.46
Fraxinus excelsior .	4,857	1.45
Carpinus betulus..	3,848	1.90

CAUSES AND INTERPRETATIONS OF BOG XEROPHYTES.

The early differences of opinion as to the effective causes of apparent xerophytic adaptations in bog-plants still persist. However, a critical study of the investigations in this field makes it evident that some views have become invalid, while others are incomplete. While further research is needed to determine quantitatively just what species are xerophytes and what are the causal relations of the various factors, it seems possible to anticipate some of these conclusions. In spite of the fact that none of the earlier studies measured the various factors concerned, they advanced nearly all of the interpretations among which choice must be made today. Although frankly puzzled by finding xerophytic devices in bogs, Volkens thought that these might be explained by periodic drought in the upper layer of the soil. In his earlier work, Warming regarded the dry climate of polar regions as the major factor in most cases, but he explained the leaf-structure of certain swamp-sedges as a consequence of inheritance, and hence independent of the habitat. Schwendener likewise appealed to a fixed heredity in explanation of the leaf-structure of exotic grasses and sedges, and thought it probable that the same interpretation would apply to the various protective modifications found in bog-plants.

Kihlmann regarded low soil-temperatures and strong drying winds as the primary factors in producing the xeroid adaptations of bog and swamp plants, but admitted that some species of the most exposed situations lacked such devices, assuming in consequence that their tissues must possess a specific resistance against cold.

Stenström rejected Kihlmann's conclusion, and turned to fixity of character in evergreen shrubs especially, and to transpiration relations as affording the proper solution. On the contrary, Goebel advanced the same explanation as Kihlmann, finding the cold soil, strong winds, and rarefied air of the Paramos sufficient reason for the presence of xerophilous species.

The controlling cause of xerophytic modifications in marine swamps and solfataras was stated by Schimper to be the salt-content, and in glacial alpine soils the low temperature. Warming considered free humous acids as the chief factors in producing bog xerophytes, as these were thought to depress the root's activity, but he included low soil-temperatures, poor aeration, water-retention by the peat, chemical substances, and a transpiration optimum as factors playing some part in the result. In connection with the concept of physiological dryness, Schimper laid the chief emphasis upon the presence of humous acids and salts and upon low temperatures as the causes of xerophytism in bogs and swamps, though it is significant that he carried out no investigations with reference to the former. It has already been suggested that this was due to a typographic error in the case of humous acids, while the retarding effect of humous salts upon transpiration was accepted upon the evidence furnished by Burgerstein, which Livingston, Transeau, and others have since shown to be insufficient, as indicated later.

The error made in Pfeffer's Plant Physiology with respect to Burgerstein's results has been so generally followed that it is desirable to give a brief summary of these.

Burgerstein (1876 : 191) demonstrated that 0.15 per cent nitric acid increased the transpiration of corn plants about 10 per cent, and 0.3 per cent, about 30 per cent in comparison with distilled water. Oxalic acid in solutions of 0.25, 0.5, and 1 per cent produced increases of approximately 65, 200, and 0 per cent in the water-loss of corn, while the two higher concentrations effected an increase of 60 and 100 per cent in the transpiration of branches of *Taxus*. Tartaric acid in 0.25 per cent solution increased water-loss in corn 20 per cent, while the 0.5 per cent decreased it about 15 per cent. As has been indicated earlier, carbonic acid usually increased transpiration. Potassium and sodium hydroxid, and ammonia in concentrations of 0.02 and 0.1 per cent regularly decreased transpiration from 15 to 40 per cent. A number of salts, viz, calcium nitrate, potassium nitrate, acid potassium phosphate, magnesium sulphate, ammonium nitrate, ammonium sulphate, sodium chloride, and potassium carbonate, regularly promoted transpiration in strengths of 0.05 to 0.25 per cent and as regularly retarded it in solutions of 0.33 to 1 per cent. Nutrient solutions of 0.05 to 0.26 per cent decreased water-loss from about 7 to 45 per cent, while humous extracts containing about 0.06 per cent of solids depressed transpiration to about the same degree.

It would appear that Früh and Schröter regarded the absence of oxygen as the primary factor in bogs and the water-retaining power of peat and the low soil-temperatures as contributing factors.

Clements questioned the views of Schimper as to the importance of humous acids and pointed out that weak solutions of acid in the

soil should promote rather than retard transpiration. He demonstrated experimentally that *Sagittaria latifolia* and *Ranunculus sceleratus* were hydrophytes, and concluded that this was true of most bog and swamp species. Their xerophytic features were regarded as stable structures that had persisted since the much earlier period when the habitat itself was xerophytic.

While Whitford (1901 : 314) regarded the accumulation of humous acids and insufficient aeration as the probable factors concerned, he emphasized the importance of the latter, owing to its preventing the healthy growth of the root-system and the presence of nitrifying bacteria. These are necessary to convert organic matter into nitrates, and hence organic decay is retarded or ceases in their absence, with the consequent accumulation so characteristic of peat-bogs.

Livingston (1904 : 383) assumed that if physiological dryness were due to humous acids or salts, these might check absorption physically by high osmotic pressure or chemically by their toxic or stimulating action. The osmotic pressure of bog-water from a number of localities was determined, and it was found that bog-waters do not have an appreciably higher concentration of dissolved substances than lakes and streams of the same region. Moreover, the same bog showed practically no difference in the amount of dissolved material found in the driest part of the summer and in winter. In further studies (1905 : 348) the conclusion was reached that some bog-waters contain chemical substances that produce the palmella stage of *Stigeoclonium*, as do solutions of poisons and those of high osmotic pressure, but such substances are not directly related to the acidity. The response to bog-water and cold closely resembled that produced in *Rumex* by Transeau. The stimulating substances were most abundant in communities most definitely of the bog type, and the amount was roughly porportional to the extent of xerophily in the vegetation. However, the results are somewhat obscured by the fact that some of the plants regarded as xerophytic, e. g., *Eriophorum*, *Typha*, and *Larix*, are actually hydrophytes or mesophytes.

Transeau (1905 : 408) has given a comprehensive account of the factors in bog habitats, which is of exceptional value because of the large amount of experimental evidence. His results showed that bog-water itself had no tendency to produce xerophytic modifications, but that low soil-temperatures and lack of aeration caused a reduction in the growth of several plant organs. When these two factors acted together, the effect was very marked. Experiments with *Rumex acetosella* showed that nearly all the characteristics of bog-plants could be developed by lowering the soil temperature, preventing proper aeration, or by growing plants in dry sand. Thus, while an undrained peat substratum may cause xerophilous structures, this is due to lack of aeration rather than acidity, which may, however, be a factor in the competition between different species for possession of the bog

areas. While the temperatures in southern Michigan are regarded as inadequate to render cold a factor in xerophily, it is probably a powerful factor further north, an assumption borne out by the bogs of northern Minnesota in which ice persists at certain depths until midsummer or later. The high water capacity of peat is a factor of some importance, in that it serves to prevent proper aeration of the substratum. The activity of nitrifying bacteria is almost completely inhibited in natural bog-soils, owing to the acidity, deficiency in oxygen, and low temperatures, and denitrification often further reduces the supply of available nitrogen.

Davis (1907) ascribed the xerophytic nature of bog-plants to the tenacity with which peat retains water, as a consequence of which plants wilt in it at 49.7 parts of water per 100 of dry soil, and crops require more than 60 per cent of water in peat to be productive. The drying-out of the peat in years of minimum rainfall was also regarded as a factor of importance. It was noted that *Betula* and *Salix* endured a foot rise in the water-level for 3 years, while more sensitive plants perished.

Dachnowski (1908 : 134) has grown gemmæ of *Marchantia* in bog-soil extract, bog-water untreated, bog-water aerated, bog-water neutral, obtained by shaking with dry calcium carbonate and filtering, bog-water filtered, shaken with lamp-black and filtered, distilled water in which bog-plants had been grown in culture, and spring-water. In the case of water from the central zone, growth in the aerated, neutral, and filtered cultures was greater than in spring-water, while that in the extract and untreated water was much poorer. Growth in water from the maple-alder zone was best in the aerated solution, practically as good in the neutral and filtered, and but little less in the untreated and bog-plant water. Similar cultures of a number of cultivated plants gave much the same results, though the aerated solution was generally less favorable than the neutral and filtered ones. This does not seem strange, as shaking and filtering and the diffusion of the dry particles should have brought about much more effective aeration of these two cultures. The conclusion is reached that the inhibiting factors of bogs are in part injurious water-soluble substances, the toxicity of which can be corrected by aeration and by the use of calcium carbonate and lampblack. The author further says:

"It may readily be questioned whether part of the response arises from a deficiency of oxygen in the soil. The evidence obtained by Bennett is against aerotropism in roots. It follows, therefore, that results reported as due to lack of aeration in the bog substratum are really due to toxicity. Under natural conditions, the inhibiting effect is eliminated by aeration, a slow process of oxidation preventing the accumulation of injurious plant excreta in the soil. However, on account of the great demand for oxygen, this process can be carried on efficiently only near the surface."

It seems certain, however, that the lack of oxygen is the primary cause, and that the acids secreted by the roots and the deleterious substances produced by anaerobic fermentation and decomposition are the consequences of it.

In later studies (1909, 1910), Dachnowski has concluded that the contaminated condition of the agricultural soils used and the decreased activity of plants in them indicates that xerophily can not be due to acidity, lack of oxygen, or low temperatures, and that the injurious substances present in bog-water and bog-soils are at least in part the cause of xerophily and of decreased fertility. It is recognized that fertility is restored through aeration, after sufficient time has elapsed for the oxidation of the injurious bodies, and, in consequence, decrease in toxicity always follows aeration and drainage. Transpiration data obtained from wheat seedlings grown in solutions inoculated with pure cultures of bog bacteria showed reduction in varying degree, and this was confirmed by the growth, showing that the residual products of many bacteria constitute in part the toxicity of the bog habitat.

As indicated in earlier sections, Hesselmann (1910) has found that the water of peat-bogs and swampy forests is often completely free of oxygen and rarely contains more than a small amount, while it is high in streams and lakes and often approaches saturation. In consequence, he finds that swamped pine forests suffer greatly on account of the lack of oxygen, while those watered excessively by spring brooks are remarkably luxuriant, and concludes that oxygen is the paramount factor.

Burns (1911 : 105) accepted the view of Davis that xerophytic areas in peat-bogs are chiefly due to the drying of surface layers and the ability of peat to render large amounts of water non-available, though he also regarded low temperature and low air-content as secondary factors.

From a study of the bogs of Cranberry Island, Dachnowski (1911 : 147) confirmed his earlier conclusion that the limiting factor was not evaporation or temperature, but the toxicity of the substratum. The effect of the latter appears chiefly when the water-supply has become stationary, through the action of bacteria especially. The edaphic aridity of the central zone reduces absorption by the roots at the time when transpiration and growth are making greater demands, and the dwarfing of the roots diminishes it still further. In a later paper (1912 : 513), the character of the obligate bacterial flora and the nature of the organic compounds produced in bogs are considered to explain the xerophytic conditions. The organic products of decomposition play the controlling rôle, and cause the infertility of peat-deposits, even when these have abundant soil-air and water-content, and favoring temperature and humidity.

Gates (1914 : 483) concludes that the xerophytism of the evergreen ericads is real, and that it has been brought about primarily by winter conditions. The transpiration is lower the more xerophytic the structure of the leaves, and this is greatest in the plants most exposed to winter conditions. While the xerophytic structure also reduces water demands in the summer, it seems to be unnecessary then, for neither extreme drought in the field nor the extreme evaporating conditions of a laboratory injured the many plants of *Chamædaphne* used. On the other hand, thousands of plants were killed down to the snow-line during the continued severe dry winter-cold of 1911–12, though the average conditions of the preceding winter did not have the slightest effect. During the winter the transpiration and rate of conduction were much higher in the evergreens than in deciduous plants, while in the summer they were much higher in the herbs and deciduous woody plants than in the evergreens.

Dachnowski (1912) has brought together all of his previous results in one comprehensive account, and reaffirms his conclusions as to the fundamental rôle of toxicity and the paramount importance of bacteria in producing it. He emphasizes the inadequacy of lack of aeration and low soil-temperatures as causes of xeromorphy, but assigns much importance to the presence of oxygen in decreasing toxicity. The behavior of the roots of bog xerophytes is said not to be due to low oxygen-content, but the growth is inhibited by the reducing action of the substratum and the incomplete disintegration of organic compounds, conclusions that are not supported by the facts of anaerobic respiration. The quantity of the products of bacterial decomposition are thought to constitute a toxic, physiologically arid habitat at one stage and an available supply of plant nutrients at another stage of the process, and hence acidity, toxicity, and reducing action represent merely a stage in the decomposition of organic matter.

Rigg (1913 : 325) has found that *Tradescantia* shows stunted root-hairs when grown in bog-water, but develops normal ones in lake and spring water, as well as in water from drained or partly drained bogs. The stunting effect disappears when bog-water is diluted with an equal volume or even one-half of its volume of tap-water, and it is increased by boiling the water down to a fraction of its original amount. All of this is in harmony with the fact that many typical bog-plants have no root-hairs. The toxin or toxins in bog-water lose their effect with drainage. It is thought possible that this toxin prevents mesophytes from growing in bogs by reducing the amount of absorptive root surface. It is obvious that practically all the effects observed can be correlated with the absence of oxygen. The author's statement that the mere absence of air from water does not render it toxic must be completely revised, if toxicity is to be measured by injury and death. In a later paper it is shown that

the products of the decay of *Nymphæa* rhizomes are injurious to *Tradescantia* cuttings and to tomato, alfalfa, and corn, even in very dilute solutions, as Sherff had shown earlier. Similar results for *Tradescantia* were obtained from the decay of potatoes and turnips, and of the rhizomes of *Castalia odorata* and *Typha latifolia.*

Rigg (1916) has summarized the data collected by Cox (1910) with reference to temperature and frost in cranberry bogs in Wisconsin and has reached the following conclusions: The temperatures in both soil and air are less favorable in the bog than on adjacent hard land. In so far as a difference of temperature between air and soil is concerned, conditions in the bog are much less favorable than on land, frost sometimes remaining in the soil as late as the first of July. With respect to relative humidity and wind velocity, the conditions were less favorable to transpiration than on the neighboring land. Rigg, Trumbull, and Lincoln (1916) have studied the osmotic pressure of water from sphagnum bogs of the Puget Sound region and Alaska, and they confirm the conclusions of Livingston and Fitting that it is not a factor in the toxicity of bog-water or of the very dilute solutions arising from the decay of *Nymphæa* rhizomes.

In a related paper (1916[2]), it is suggested that low osmotic pressure of bog-water indicates that the material in solution in it is probably in a colloidal state. The data presented are regarded as confirming this view and warranting the suggestion that this colloidal matter is a large factor in the toxicity of the water.

Rigg (1916[4]) has made a comprehensive summary of the theories advanced to explain bog xerophytes, and indicates that part of the discrepancy in opinion is due to various definitions of bog-plants. While this is true in some degree, it seems unavoidable that the views of Volkens, Warming, Schwendener, Kihlmann, Goebel, Stenström, Schimper, and others must be examined in the light of the species that they regarded as bog xerophytes, which are much more numerous than those recognized by Rigg.

Clements (1916 : 90) has concluded that most of the xeroid species of wet places are not xerophytic at all, but that a restricted group characteristic of peat-bogs and heath-moors are actual xerophytes. No final decision with respect to these was regarded as possible, however, until their water requirements are studied experimentally and their transpiration response known. The conclusion was reached that lack of oxygen is the primary factor in bogs, and the acid a consequence or concomitant. This view was later amplified (1920: 85), and the presence of acids and bog toxins was attributed to the direct activity of the roots and the bog flora under conditions of deficient aeration.

Bergman (1920 : 13) has observed that growth is reduced in plants with roots submerged in *Sphagnum* as compared with peat, and ascribes this to the greater lack of oxygen in the former. When

aeration is provided, the development of plants is essentially as good in bog-water as in nutrient solution. The oxygen-content of bog-water decreases and the carbon dioxid increases from the *Carex* to the *Chamædaphne-Andromeda* and the *Larix-Picea* stages. The adjustment of the roots of bog-plants to the water-level is due to the need of securing a sufficient supply of oxygen. In a later paper (1921 : 50), he has found that the injury of cranberry vines as a result of flooding is due to the lack of oxygen, and that injury is most frequent during cloudy weather, when the oxygen-content is the lowest.

ACIDITY.

While the scope of the present treatment does not permit a comprehensive account of the numerous studies of soil acidity, it seems desirable to deal with the more recent investigations, because of the light they throw upon acidity in bogs and upon soil toxins. Ecological studies of acidity have been few, and the paucity of experimental results makes it impossible to determine whether acidity is a cause or merely a concomitant (Fernald, 1907; Coville, 1910, 1913; Sampson, 1912; Wherry, 1920). Practically all of the quantitative and experimental studies of acid soils have been made by chemists, and the value of the results has been somewhat obscured by the general lack of physiological and ecological knowledge. In spite of their great divergence as to the causes of acidity, nearly all of them are valuable in helping to determine quantitative relations, and some of them are of the first importance to ecological investigation.

The theory that soil acidity is due to the accumulation of insoluble organic compounds, the so-called humic acids, has been generally accepted until the last decade or two. Sprengel (1826) isolated a substance from soil that he called humic acid, and Berzelius (1838) obtained this acid and the related humin from the treatment of soil with an acid. Mulder (1840) recognized 7 different organic substances in the soil, namely, ulmic, humic, geic, apocrenic, and crenic acids, regarded as successive steps in the decay of organic matter in the soil, and humin and ulmin. Eggertz (1889) threw doubt upon the existence of humic acids by showing their variability of composition. Van Bemmeln (1888) contended that humic acids were not definite compounds and that their formulæ were without value. He regarded humus substances as colloidal in nature and the humates as adsorption compounds. This view has received the support of many chemists, and it has apparently been confirmed for the acidity of sphagnum bogs by Baumann and Gully (1910 : 47), who stated that no free humic acids are to be found in peat-moss. They contend that the acidity of sphagnum and peat soils generally is due to the colloids of the external walls of the sphag-

num cells. This view has been vigorously assailed by Tacke and Süchting (1911), as well as many other chemists, who maintain that acid soils exhibit phenomena to be explained only by the presence of true acids. Schreiner and Shorey (1909) have discussed the results obtained by workers in this field, and lend their support to the conclusion of Cameron and Bell (1907) that the existence of humic acids has never been demonstrated and no satisfactory descriptions have ever been given of their physical or chemical properties or of their salts or characteristic derivatives. Their effect upon plants, whether harmful or otherwise, is considered to be as doubtful as their constitution or composition.

Blair and Macy (1908) concluded that agencies are at work producing acids in practically all cultivated soils, and these tend to become permanently acid unless bases are present in sufficient quantity. The acids may be the result of decomposing organic matter, of bacterial action, or of the breaking-up of commercial fertilizers. They may exert a directly injurious effect upon the plants themselves, or upon beneficial bacteria, or they may bring into solution mineral compounds that are injurious to the plants or the bacteria.

Abbott, Conner, and Smalley (1913) have found that peat soils typically dominated by huckleberries are excessively acid and poorly supplied with lime. The water extract contained very large amounts of aluminum salts, highly poisonous to corn seedlings. These facts seem to warrant the conclusion that the unproductivity of such acid marsh soils is due to the toxic action of soluble salts of aluminum, or rather to the acid conditions that permit these salts to exist.

Ruprecht (1915 : 128) has shown that aluminum sulphate is very toxic to clover seedlings in culture solutions containing more than 40 parts per million and that ferrous sulphate is toxic in concentrations greater than 4 parts per million. The toxic effect of both can largely be remedied by calcium carbonate up to a certain point, but not by calcium sulphate. It is assumed that the carbonate precipitates the aluminum and the iron as hydroxids, thus removing them from solution and counteracting their harmful effect, the difference between the two being due to the different solubility of the hydroxids. The toxic action is restricted to the outer layer or two of the apical region of the root, thus retarding or arresting the growth of the latter.

Truog (1916) has found considerable amounts of manganese in the soil solution of certain acid soils, and thinks that this element may sometimes act injuriously as a result of high absorption.

Wilcox and Kelley (1912), White (1916), and Johnson (1917) have similarly shown that manganese is toxic under certain conditions. When lime is added to such soils, the amount of manganese in the soil solution is inconsiderable, as the alkaline condition favors its precipitation.

Ruprecht and Morse (1917) state that the positive presence of soluble salts of iron, aluminum, and manganese in soils which have been repeatedly dressed with ammonium sulphate without adding lime; the formation of one or more of these salts in soils that were extracted with solutions of ammonium sulphate; and the positively injurious action of manganese sulphate, iron sulphate, and aluminum sulphate form a chain of facts which clearly indicates that the injurious effects of sulphate of ammonia when used freely without the accompaniment of lime are due to the formation of these soluble salts in the soils of the fields so dressed.

Hartwell and Pember (1918 : 276) have determined that the unlike response of rye and barley to acid soil is due to active aluminum. Treatment of an acid soil with phosphoric oxide or acid phosphate reduced the amount of active aluminum in the soil, and large additions of the latter caused remarkable growth in plants in which previously growth was impossible. This was in spite of the fact that the acid phosphate greatly increased the acidity of the soil; however, it much decreased the active aluminum. It is suggested that the practical advantage of phosphate and lime may be due to the precipitation of active aluminum, quite as much as to the value of the first as a nutrient and the second as a reducer of acidity.

In similar studies of the toxicity of aluminum, Mirasol (1920 : 153) has shown that its salts are directly concerned in the unproductivity of acid loam soils. In soils with sufficient calcium, toxic aluminum salts may never be formed, but in acid soils, where the bases are deficient, such salts are largely the end-products of sulfofication and nitrification. The toxicity of aluminum salts is corrected by calcium carbonate or by acid phosphate through their precipitation as insoluble calcium aluminate or aluminum phosphates.

In studies of an acid soil in Assam, Meggitt (1914) has concluded that the acidity is partly due to specifically toxic organic compounds, arising in consequence of reduced oxidation in the soil. Such toxic organic compounds are destroyed by oxidation, and this is promoted by lime, nitrates, or phosphates, whether it is carried on by the roots themselves or by other organisms.

Harris (1914 : 14) concludes that the behavior of the soil toward neutral salts is not due to insoluble humic acids or to the presence of organic matter, but to inorganic compounds, probably hydrated silicates. The reaction of so-called acid soils of the sandy-loam type is due to the selective adsorption by the soil of the basic constituents of the neutral salt solution, and is not caused by double decomposition with adsorbed acids or insoluble "humic acids." The "acidity" of soils of this type probably arises from the formation of soluble salts through the interaction of weak acids ($C_2H_2O_4$, CO_2, etc.) in the soil solution and the basic material naturally held absorbed by

the soil, and their subsequent removal by leaching, thus leaving the soil free to absorb more basic material from any source with which it may come in contact.

Truog (1914 : 505) states that he is even more adverse to accepting the colloid-absorption theory in explanation of soil acidity than the so-called humic-acid theory. While the acidity of peat and muck soils is undoubtedly due in part to organic acids, there are upland soils practically free from organic matter that react strongly acid. It is assumed that this inorganic acidity is due to the reaction of the water solution with the silicates, which forms a soluble hydroxid or salt taken up by plants or removed by drainage, and a comparatively insoluble acid silicate that accumulates in the soil to produce acidity. By means of a special method it has been found that it makes little difference whether calcium, barium or sodium hydroxid is used to neutralize acidity, thus indicating strongly that this is due to true acids and not colloids, since the latter should demand different amounts. While there is no question that colloids exist in soils, some absorbing bases and others acid-ions, the amount of absorption in the case of the laboratory study of pure colloids is comparatively very small, and the absorption capacity of these colloids is practically a negligible factor in soil acidity.

In a comprehensive discussion of sour soils and liming, Frear (1915 : 81) has considered the various causes of soil acidity, apparently assigning some value to all of them, but giving the primary rôle to humous compounds. The other causes discussed are: (1) leaching of basic material by waters containing carbonic acid; (2) acid silicates; (3) iron pyrites; (4) furnace and coke-oven fumes; (5) aluminum salts; (6) decay of plant residues; (7) fermentation in the soil; (8) fertilizers; (9) physiological acidity; (10) sulphur fungicides.

Truog and Sykora (1917 : 348) conclude that chemical reactions probably play as important a rôle as such physical phenomena as adsorption and possibly have even a greater effect. Calcium carbonate, acid kaolin, and other silicates are especially important in this connection. The chemical and physical constitution of most agricultural soils seems to be such that the injurious action of toxins present or arising in various ways is entirely or largely prevented by proper tillage and the use of lime when needed.

Conner (1918 : 328) has shown that the acidity of soils varies with the water-content, the acidity being greater in soils kept at half than at fourth saturation. Soils high in organic matter showed the greatest acidity at full saturation. The measurable acidity of acid soils varied much under different conditions of moisture and aeration, owing to chemical rather than physical changes. The water-content of acid soils is acid in reaction as shown by determination of the hydrogen-ions. Acidity in wet soils may be caused by the

leaching of basic elements in drainage-water, or the removal of bases by crops, by the decay of carbonaceous and nitrogenous substances, and by the hydrolysis of mineral compounds and organic matter.

Hoagland and Sharp (1918 : 139) define soil acidity as that condition of the soil in which its aqueous solution contains H-ions in excess of OH-ions. The H-ion concentration of suspensions of acid soils is not markedly affected by increasing the content of carbon dioxid up to 10 per cent, but it is slightly increased in alkaline soils, and a notable increase occurs in soils containing alkali carbonates. No treatment with carbon dioxid produced an alkaline reaction in the suspension of an acid soil. When the original conditions were restored, no permanent change in the soil reaction could be ascribed to the carbon dioxid.

Sharp and Hoagland (1919 : 197) have found large inversion of sugar only in soils of distinctly acid reaction, the greatest inversion coinciding with the highest H-ion concentration of the soil suspension as well as of the water and the sugar extracts. Direct evidence was also obtained that acid soils do give acid filtrates, the acid reactions of which were generally of a magnitude very similar to those obtained with the suspensions.

Noyes and Yoder (1918 : 151) state that organic matter is acid in reaction at certain stages of decay and that apparently no work absolutely proves that this acidity is other than carbonic acid weakly held by the organic matter. They find that acid soil increases in acidity by standing in the greenhouse with one-half its water-holding capacity satisfied. Cropping brought about a slight increase in acidity, while applications of carbon dioxid increased it further, constant treatment giving the greatest amount. Thus, carbon dioxid added to cropped soil increased its acidity, whether it was treated with lime alone or lime and fertilizer. The results support the chemical theories of soil acidity, since different applications of carbon dioxid gas, which is not only soluble in water but also combines with it, yielding hydrogen-ions, caused differences in acidity.

Plummer (1918 : 30) has found that ammonium sulphate materially increases the acidity of the soil as measured by the hydrogen-ion concentration, while the effect of potassium sulphate is somewhat less. Sodium nitrate reduced acidity slightly, acid phosphate seemed without effect, and lime materially increased the OH-ion concentration of field plots.

Rice and Osugi (1918 : 354) state that "soil acidity" is the term customarily applied when infertility of the soil can be corrected by the use of a free base such as lime. There are many factors involved in causing this condition in soils, the presence of real acid being but one of them. The methods used for determining "soil acidity" generally do not measure the acid, but depend upon properties of the soil-mass unrelated to acidity. The power of a soil to catalyze

the reaction of cane-sugar inversion is a measure of its acid, and is probably the only method that can measure the acid bound up with the solid soil phase.

Walker (1920) has found that more acidity was developed in muck soil under water-soaked anaerobic conditions than when the moist soil was kept aerated by stirring. This agrees with Conner's results to the effect that a peat soil develops more acid the more water it contains. In this case, the drier soils are better aerated by diffusion than the wetter ones, and the oxidation thus made possible decreases the acidity.

Wherry (1920 : 164) regards soil acidity as probably a rather complex phenomenon, and states that it is misleading to look to a single substance or type of substances as the source of hydrogen-ion producing it in all cases. It seems probable that comparatively few of the possible sources of hydrogen-ion, and hence of acidity, coexist in appreciable amounts in any one soil. A statement is given of the various sources of hydrogen-ion, as follows:

Soil constituents yielding hydrogen-ion.

1. Directly (when treated with water alone).

A. Inorganic:
   a. Strong, highly ionized acids, like hydrochloric, sulfuric, etc.
   b. Weak, slightly ionized acids, especially carbonic.
   c. Acid salts, like potassium acid sulphate, which may be moderately or slightly ionized (as acids).
   d. Salts of weak bases with strong acids, like aluminum chloride, ammonium sulphate, etc., which are slightly hydrolyzed and therefore yield a small amount of hydrogen-ion.

B. Organic:
   a. Strong, highly ionized acids, like oxalic.
   b. Weak, slightly ionized acids, like acetic.
   c. Acid salts, like potassium acid sulphate, which may be moderately or slightly ionized (as acids).
   d. Salts of weak bases with strong acids, like aluminum citrate, ammonium oxalate, etc., which are hydrolyzed as in A *d*.
   e. Amino acids, like aspartic (aminosuccinic) acid, which are internal salts in the sense that the acidity is neutralized by the amino group, and which may be moderately or slightly ionized.
   f. Humic acids, which if they exist at all are slightly ionized.

2. Indirectly (when treated with solutions of salts).

A. Inorganic, especially colloidal clay.
B. Organic, especially colloidal humus.

Gillespie (1916) has investigated the hydrogen-ion concentration of 22 soils in water suspensions and found the range of H-ions to be from pH 4.4 to pH 8.6.

Sharp and Hoagland (1916 : 123) have measured the acidity of 24 different soils by means of the hydrogen electrode, certain of them giving an H-ion concentration as high as 0.2×10^{-3} and hence possessing a considerable intensity of acidity. The hydrogen-ion concentration of different soil suspensions varied within wide limits,

from a condition of high acidity to one of high alkalinity, namely, from pH 3.7 to pH 9.7. The conclusion is reached that soil acidity is due to the presence of an excess of hydrogen-ions in the soil solution, direct evidence of which fact is given by hydrogen-electrode measurements. This confirms the view that soil acidity is fundamentally dependent upon the equilibria of reactions yielding an excess of H-ions, and is not necessarily related to the phenomena known as "absorption" and "adsorption," in conformity with the opinions of Loew, Hanley, Gillespie, and Truog.

Plummer (1918 : 19) has determined the hydrogen-ion concentration of soil suspensions of 68 samples of soils from the southeastern United States. Excessive acidity was found in the Norfolk silt loam and in the mucks, reaching values of 0.1×10^{-3} and 0.2×10^{-1} respectively. Truog and Loomis (1918) have found a range of 4.5 to 8.0 in the hydrogen-ion exponents for a number of the common cultivated acid soils of Wisconsin.

Hoagland (1917 : 547) has grown barley seedlings in partial nutrient solutions of like osmotic pressure, but with a considerable range of H-ion and OH-ion concentrations, and found that the OH-ion was relatively much more toxic. When the concentration of the OH-ion was greater than 1.8×10^{-6}, the effect was distinctly injurious, and above 2.5×10^{-5} extremely toxic. With an H-ion concentration of approximately 0.7×10^{-5}, growth was favored, but one of 0.3×10^{-3} was very toxic. These results are not in accord with those of Hartwell and Pember (1907), Breazeale and LeClerc (1912), Dachnowski (1914), and Miyake (1914), all of whom found the H-ion to be more toxic, but these are explained as due to the fact that dilute solutions of potassium or sodium hydroxid do not give the effect of the OH-ion concentration on plant-growth.

In later studies (1918 : 422), plants exhibited a strong tendency to change the reaction of various potassium phosphate solutions toward neutral, acid, and alkaline solutions, soon reaching a point about equivalent to pH 7.0, and neutral ones remaining unchanged. In extensive experiments with barley and beans, nutrient solutions with acid reaction always reached a reaction approximately neutral after varying periods of contact with plant roots. When barley plants were grown in nutrient solutions and then transferred to solutions of KCl, K_2SO_4, $MgSO_4$, K_3PO_4, NH_4Cl, and $NaNO_3$, an excessive concentration of OH-ion or H-ion was nowhere found, in spite of active absorption. When an acid reaction was present, it was due to slightly dissociated acids, usually carbonic, to acid salts in the case of NH_4Cl solution, and possibly in some cases to organic acids. In spite of the assumption that most crop plants require a slightly alkaline soil solution, a reaction of pH 5.0 was found to be in nowise injurious to barley seedlings or to beans, thus supporting the view of Truog that acidity itself is not the limiting factor. In California

peat soils that are decidedly acid (pH 5.4 to 4.5), excellent crops of barley, oats, beans, potatoes, onions, corn, asparagus, etc., were produced, showing that the acidity did not interfere with growth or with the formation of nitrates.

Duggar (1920: 1) has studied the growth of seedlings of wheat, corn, and field peas in relation to H-ion concentration and the composition of the nutrient solution. Theoretically, the solutions possessed a pH exponent of about 4.5, but solution B in particular varied from pH 5.4 to pH 7.1. Under the most favorable conditions the 3 solutions all gave excellent growth, but under extreme conditions, producing high evaporation, it became important to correct to the higher pH exponent. The sensitivity to high H-ion concentration is in the order of wheat, corn, and peas. In general it seemed that there was no single "best" solution for the 3 plants used, but there is a considerable range of salt or ion proportions within the "optimum" concentration. If the initial pH of the culture solution is considerably less than neutral, there is a general tendency for this to be shifted toward the neutral point.

In a series of papers, Truog (1918, 1919) has given an illuminating discussion of the relation of acidity to the growth of plants, which is of such importance as to warrant quoting the summary in its entirety:

"With a few exceptions agricultural plants grow best on soils well supplied with readily available lime. To be readily available, lime may exist either as the carbonate, as an easily hydrolyzable silicate or salt, or as a constituent of easily decomposable organic matter. The classification of agricultural plants as being lime-loving, lime-avoiding and indifferent, or as being acid-intolerant, acid-tolerant and indifferent, leads to confusion and gives the wrong impression regarding the relation of lime and soil acidity to plant growth. The subject is very complex and, as has been indicated, soil acidity has many indirect and general influences on soil fertility due to its effect on physical, chemical, and biological conditions of the soil.

"It is well known that an acid condition is unfavorable to the highest development of desirable physical and biological soil conditions. An acid condition usually lowers the availability of nearly all the essential elements. On the other hand, soil acidity usually favors the accumulation and solubility of toxic organic and inorganic substances. Among these toxic substances soluble aluminum salts have been noted by a number of investigators, and possibly in some cases manganese salts should also be considered. In certain unusual cases of soil acidity sufficient amounts of these toxic substances may be present to be very harmful to some plants. The relation of soil acidity and liming to malnutrition due to a lack of iron in the plant, to plant diseases and to plant competition also need to be considered in a few special cases, particularly in cases where soil acidity appears to be a favorable condition.

"Besides the indirect influences which affect all plants, and some probably to a considerable extent, soil acidity has a specific influence which affects some plants like alfalfa and sugar beets very much more than others, like cowpeas, potatoes, and oats. At various times this specific influence of soil acidity has been ascribed to at least three causes: viz., (*a*) its effect on the supply of available calcium needed by plants as direct plant-food material,

(*b*) its effect on the symbiotic nitrogen-fixing bacteria, (*c*) and its toxic or destructive effect on the root tissues of plants.

"The supply of available calcium in all forms becomes less as soils become acid, but usually there is still sufficient present to furnish that needed as direct plant-food material. Since the symbiotic nitrogen-fixing bacteria live in the nodules, soil acidity can not affect them directly, except before they enter into symbiosis, when it may lessen their activity and delay the time of infection. Since the relation of non-legumes to soil acidity runs parallel with the relation of the legumes, it follows that the direct influence is not on the legume bacteria but on the plants themselves.

"That this direct effect on the plants is not often due to a destructive action of the acidity on the root tissues is evident from the fact that experiments have shown that plant roots are unaffected by solutions of a higher acidity than that of most acid soil solutions. This is further substantiated by the fact that the acidity (H-ion concentration) of the sap of most plants is of the same order as that of the soil solution of most acid soils, indicating that similar processes are probably at work in the two cases, as a result of certain analogous conditions which exercise a regulatory function in this respect. It is undoubtedly largely proteins in the case of plants, and colloidal organic and inorganic matter, especially silicates, in the case of soils which act as "buffers" and thus bring about this regulation of acidity to a considerable extent, preventing rapid changes and unusually high degrees of soluble acidity.

"In most cases it thus appears that the main specific harmful influence of soil acidity on certain plants is not due to any of the three suggested reasons, but to its influences in preventing these plants from getting at a sufficiently rapid rate the calcium as the carbonate or bi-carbonate which is needed to neutralize and precipitate certain acids in the plants themselves, which are probably largely by-products, produced as the result of certain vital reactions in the growth of plants. If calcium in these forms is not furnished at a sufficiently rapid rate, then the rate of these reactions is lowered accordingly as is also the rate of plant growth.

"Each species of plant has a certain lime requirement which must be satisfied for maximum plant growth and this lime requirement is defined by the writer as follows: The expression 'lime requirement' of a plant refers to the actual lime needs of the plant itself, especially as to the ease and rate at which lime must be secured from the soil by the plant for normal growth. Thus if a plant has a high lime requirement, then the solution and delivery must be rapid and easy in order to meet the needs of the plant.

"The three main factors which determine the lime requirement of a plant are: (*a*) lime content, (*b*) rate of growth, and (*c*) feeding power of the plant for lime. The first two factors operate in one direction while the third operates in the opposite direction. That is, the higher the lime content and the rate of growth, the higher will be the lime requirement, and conversely. Also, the higher the feeding power for lime, the lower will be the lime requirement, and conversely. The resultant of these three gives the lime requirement of the plant. A simple method of expressing these factors and obtaining the resultant is described in this article.

"A table is also given in which are expressed the lime requirements of 62 species of plants as obtained by this method. These lime requirements are compared with corresponding figures which represent the relative response of these plants to the liming of acid soils, or reciprocally to their ability to grow on acid soils. The comparison reveals a close correspondence and hence substantiates the theory which has been proposed that, usually, the main specific injury of soil acidity is that it prevents plants, especially those with

high lime requirements and relatively weak feeding powers, from getting the lime from the soil at a sufficiently rapid rate to meet their needs. This is further substantiated by the parallel relation found between the amount of growth of alfalfa on acid soils and the amount of calcium which could be extracted with carbonated water from these soils. These considerations are especially important in formulating a practical system of using lime, especially as regards the amount to be used which, as is discussed in detail, is dependent on the lime-requirement of the crop, the degree of acidity of the soil, and the fertility of the soil."

Truog and Meacham (1919 : 469) have found the acidity of the cell-sap of various plants to vary from pH 6 to pH 4 and to be regularly greater in the case of plants grown on unlimed acid soil than in those on limed acid soil. The juice from plants cut in the morning was more acid than that of plants cut later in the day, indicating an accumulation of acids at night, and it was also more acid during warm, dry weather than after a heavy rain. For each species there is a certain acidity most favorable for the life processes, and in many cases soil acidity affects the acidity of the sap by limiting the supply of lime available. Lime and other bases are needed to neutralize the acids formed during metabolism, some of which are mere by-products. If the supply of bases is inadequate, the acidity of the sap rises to a point where the accumulation of acids limits the processes that produce them. While such a condition of self-regulation probably prevents death from over-acidity, slow growth and a weakened condition result in the case of plants of high lime requirement when grown on acid soils.

Truog (1918 : 177) points out that the acidity of the plant-sap is of the same order as that of the water extracts of acid soils, and hence it is not to be expected that the acidity of such soils often becomes high enough to be directly of serious injury to plant roots.

Haas (1916 : 233) has demonstrated that the cell-sap of normal cells is often decidedly acid (pH 3), contrary to the accepted view that the cell-sap must be neutral or nearly so for normal physiological functioning. Moreover, the blue coloring of living cells does not indicate an alkaline reaction, but one decidedly acid to neutral or barely alkaline (pH 3 to pH 8). The reaction of the cell may change from pH 3 to pH 7 as it dies.

In reviewing Hartwell and Pember's work, Crocker (1919) states that the hydrogen-ion concentration found in acid soils by the gas method is generally but a fraction of that necessary to reduce the growth of plants in water or sand cultures.

The extent to which competition is a decisive factor in the apparent preference of many native species for acid soils is indicated by the behavior of sorrel, *Rumex acetosella*, which has perhaps received the most attention experimentally. Tacke (1910) stated that sorrel did as well on plats heavily limed as upon acid soils, while Wheeler (1905) reported that lime seemed to be unfavorable to the growth of

sorrel, owing to the fact that it brought about conditions favorable to clover and other plants, which were then successful in the competition.

White (1915), in dealing with soil rendered very acid by ammonium sulphate, showed that sorrel was largely replaced by clover where limestone was present in slight excess, but that it also gave the highest yield with the maximum amount of limestone. The calcium-content of sorrel in acid soil was but 10 per cent of that in alkaline soil. The conclusion was reached that sorrel is not an acid-loving plant, but that it is able to adapt itself to conditions unfavorable to most field crops. It invaded the acid plat not because of preference for an acid soil, but because of the opportunity for establishment afforded by the failure of the clover.

Pipal (1916) has found that lime exerts no harmful effect upon the growth of sorrel. Wherever acidity or other conditions unfavorable to crop plants occur, sorrel takes possession at the expense of the crop, but if the unfavorable factor is corrected by means of limestone, manure, drainage, etc., crop plants are enabled to compete successfully with sorrel. Frear (1915 : 109) has discussed the results of White and others with respect to sorrel and various crop plants.

Wherry (1920) has studied the distribution of plants around salt marshes with respect to soil acidity, and concludes that the latter is a factor of considerable if not fundamental importance. It is not regarded as the only factor of importance, nor is it implied that the acid or alkali acts directly upon the plant. It is thought that some plants may require a soil of definite acidity or alkalinity for themselves or for symbiotic organisms, while others may be favorably affected by some property of the soil that accompanies acidity, and still others may find competition less severe in soils of a certain degree of acidity. The presence of species in soils with an acidity of 300 is assumed to be a matter of preference and not merely of tolerance, since the majority of them are not known to grow in much lower degrees of acidity. However, it is interesting and perhaps significant that at least one-third of the species listed often grow in soil but weakly acid or even somewhat alkaline.

Summary.—The causes of soil acidity are still a subject of earnest debate, and much more investigation is needed before a final decision is possible. However, there is a strong tendency to recognize multiple causes, as has been done by Blair and Macy, Frear, and Wherry especially, though there is great difference of opinion as to which of these is paramount. Of all the authors considered, Frear is the only one that regards humus as a factor in acidity. The view that acidity is due to adsorption is maintained by Cameron, Harris, and Bogue, and this process is regarded as one of the factors by Frear and by Wherry. Veitch, Daikuhara, Conner, and Rice consider the re-

placement of weak bases by strong ones, with resulting hydrolysis, as primarily responsible for acidity, while Hanley, Truog, Gillespie, Sharp and Hoagland, and Plummer ascribe it to the presence of soluble acids, and Loew invokes both factors.

The manner in which acid soils work injury to plants still demands much study, but at least three methods seem highly probable. In muck soils and in bogs it appears certain that the lack of oxygen and the accumulation of carbon dioxid are the primary factors, while the organic acids and salts resulting from anaerobiosis probably play some part also. In some soils acidity brings salts of aluminum, manganese, or iron into solution, and the toxic effect is then exerted by these. This has been demonstrated by Blair and Macy and by Ruprecht and Morse for all three elements, by Abbott, Conner and Smalley, Daikuhara, Frear, Ruprecht, Miyake, Funchess, Hartwell and Pember, and Mirasol for aluminum, and by Wilcox and Kelley, Truog, White, and Johnson for manganese. In general, the harmful influence of acidity is explained by Truog as due to its effect in preventing certain plants from getting the calcium needed for neutralizing the organic acids produced in metabolism at a rate sufficiently rapid, thus leading to the lowering of both metabolism and growth.

The frequent assumption that acidity itself is injurious is not borne out by the results of Hoagland, who found that a large number of plants gave excellent crops in soils with pH 5.4 to pH 4.5. Haas found the acidity of cell-sap to be often as high as pH 3, and Truog and Meacham as high as pH 4. The highest H-ion concentration found in acid soils by Truog and Loomis was pH 4.5 and by Gillespie, pH 4.4, while Sharp and Hoagland obtained a maximum of pH 3.7, and Plummer found greater concentrations only in muck soil. Hence, the statement of Truog that the acidity of soils is not often high enough to directly injure plant roots seems to be entirely warranted. Even in muck soils it is probable that acidity is a consequence of anaerobic respiration, and thus an effect rather than a cause.

CONCLUSIONS.

Great divergence of opinion has prevailed with respect to the causes of the xerophilous appearance of bog and swamp plants. The great majority of the views have been derived from observation rather than from the measurement of habitat factors and actual experiment. With the increase of experimental study, the task of assigning the proper value to each factor suggested has become much easier, but further research is needed to determine the mutual relations of the primary factors. The value assigned to humic acids and humates by Warming, Schimper, and Whitford has not been accepted by other workers, and little importance has been given to periodic drought in bogs, as suggested by Volkens, Davis, and Burns,

or to the water-retaining power of peat, advanced by Warming, Früh and Schröter, Davis, and Burns. Low temperature has generally been recognized as a primary factor in boreal, polar, and alpine bogs, following the conclusions of Kihlmann, Schimper, Goebel, Warming, Meigen, Früh and Schröter, Transeau, Burns, and others. This is confirmed from another direction by Gates's demonstration that the bog evergreens are winter xerophytes.

The oxygen-content of the soil has been regarded as the controlling factor by Hesselmann, Clements, and Bergman, and as a primary factor by Warming, Früh and Schröter, Whitford, Transeau, Coville, and Burns. The importance of toxic compounds, which is an outcome of the earlier view that humic acids were a factor, was first suggested by Livingston, and has been advocated chiefly by Dachnowski and by Rigg. Finally, Clements has maintained that most so-called bog xerophytes are not xerophytes at all, but hydrophytes or rarely mesophytes that owe their peculiar impress to the stability of ancestral characters. Similar views as to the significance of fixed characters were early advanced by Warming for certain sedges, by Schwendener for xeroid sedges and grasses, and by Stenström for the evergreen bog plants.

The work of Clements, Sampson and Allen, Gates, Otis, Folsom, Dosdall, Bergman, and Clements and Goldsmith has shown that a large number of the so-called bog xerophytes are hydrophytes. It clearly indicates that the greater number of the bog xerophytes listed by Kihlmann and by Warming will prove to be hydrophytes when their water-relations are determined. In fact, it appears probable that the term "bog xerophyte" will finally be restricted to the broad-leaved evergreen ericads and similar plants, whose xerophily has been shown by Gates to be due to winter rather than to the direct action of bog conditions. The species of supposed bog xerophytes as listed by Warming and others that have been shown to be hydrophytes are the following: *Sagittaria latifolia*, *Ranunculus sceleratus*, *Scirpus lacustris*, *Carex filiformis*, *Pontederia cordata*, *Scirpus americanus*, *Typha latifolia*, *T. angustifolia*, and *Equisetum fluviatile*. The results now being obtained in continuation of this study indicate that practically all helophytic sedges, grasses, rushes, alismals, thin-leaved dicotyl herbs, and deciduous shrubs will prove to be hydrophytic in their water relations.

The universal need of oxygen by flowering plants, the nature and products of anaerobic respiration, the regular presence of air-passages or aerenchyma in amphibious and floating hydrophytes, as well as of stomata constantly open, all indicate that the lack of oxygen is the controlling factor in swamps and bogs, and the presence of toxic substances a consequence of the resulting anaerobic respiration. In this, all organisms that demand oxygen, and produce alcohol, organic acids, or other deleterious substances in its absence, have a share,

whether they be chlorophyllous plants, molds, bacteria, protozoa, etc., but it is highly probable that bacteria and molds play the major rôle. As a consequence, there is nothing fundamentally antagonistic between the view that lack of oxygen is the chief factor in bogs, and the view that toxic substances play the controlling part. Both must be taken into account, but the place of first importance must be accorded to lack of oxygen, since it not only affects plants profoundly itself, but also because it bears a causal relation to the accumulation of carbon dioxid and other toxic substances.

Much additional investigation is required to determine the respective shares of the lack of oxygen alone, the accumulation of carbon dioxid, the presence of organic acids, and of other toxic compounds in the characteristic effect of bog-water. The results of many researches have shown that a deficient oxygen supply inhibits absorption, photosynthesis, respiration, tropistic response, and growth, while amounts of carbon dioxid ranging from 2 to 20 per cent produce in addition a toxic effect, which further inhibits functioning, growth, and reproduction. While the results of Hesselmann and of Bergman in particular indicate that the low oxygen-content and the corresponding abundance of carbon dioxid are sufficient to explain the effect of bog-water, studies of root excretion under anaerobic conditions, and of the effect of the organic acids excreted, make it clear that these are sometimes concerned at least.

Wehmer (1891, 1906) has shown that the oxalic acid produced by certain fungi is very toxic to plants, and Lövinson (1900 : 217) has found that solutions of formates, acetates, or propionates hindered germination, and decreased growth and functioning, as a consequence of their effect upon the protoplasm and nucleus of the root-cells. Stiehr (1903) has studied the effect of acetic, oxalic, and citric acids upon root-hairs, and finds that very dilute solutions cause the death of the root-tip and even the entire root. This result was brought about by a solution of 0.02 per cent in the case of each acid with a maximum exposure of 3 hours.

Aso (1906) has observed that sodium or calcium acetates or formates exert an injurious effect upon higher plants, similar to that produced by free acetic or formic acid. It seems certain that bogs must contain other toxic organic substances, similar to those isolated by Schreiner, Reed, Shorey, and others, from various soils, while the work of Kaserer (1905) shows that the hydrogen and methane derived from the anaerobic fermentation of cellulose inhibit nitrification, and may affect other aerobic processes.

III. TOXIC EXUDATES AND SOIL TOXINS.

Early views.—The early observations upon root excretions were made at a time when physiological knowledge was still of the vaguest, and are merely of historical interest. The first mention of root excretion seems to have been that of Hales (1727), who assumed that albumen as well as carbon dioxid was secreted by roots. Duhamel (1755) noted that the earth about the roots of old elm trees was darker and more greasy than usual, and concluded that this was the result of root secretion. Brugmans (1786) thought to see small drops exuded from the ends of roots of *Viola arvensis* grown in sand, and assumed that this peculiar sap was injurious to neighboring plants. He ascribed to *Lolium temulentum* the power of corroding the roots of nearby plants, and decided that it was a specific excretion that made *Cirsium arvense* so harmful to oats, *Euphorbia peplus* and *Scabiosa arvensis* to flax, *Erigeron acris* to wheat, *Spergula arvensis* to buckwheat, and *Inula helenium* to carrots.

Senebier (1791) and Cotta (1806) supposed that roots excreted a substance which often accumulated to the point of bringing about the decomposition of bulbs in the soil, and Simon (cf. Unger 1836) thought that the roots of hyacinth served only for purposes of excretion. Plenck (1795) believed that plants excreted refuse more or less after the manner of animals, as shown by the drops exuded at night through the "openings" of the roots. He regarded this "excrement" as partly useful, partly injurious to the plant itself, as well as to its neighbors.

Sprengel (1812) regarded the moisture about the roots of grasses as an excretion, and thought that it aided in increasing the fertility of dune-sand, a view supported by the observations of E. Meyer (1830). John (1819) found that the malic acid of hyacinth bulbs was excreted into a solution, where it converted sodium carbonate into sodium malate.

DeCandolle (1832 : 248) regarded the excretions of roots as of great importance in their economy, and believed that cockscomb and other weeds injured adjoining plants in consequence of harmful root secretions. He followed Humboldt and Plenck in assuming that such secretions were the basis of the supposed attraction and repulsion of plants as expressed in plant communities. He also ascribed the benefits of crop rotation to root excretions, on the assumption that the excretions of one crop would be harmful to the same crop, but harmless or even beneficial to a different one. He supported his conclusions by the results of Macaire (1832), who thought to demonstrate that the roots of grains, grasses, and other plants excreted gummy substances, calcium carbonate, etc. These excretions were assumed to free the plant from substances that could not

be assimilated or might prove injurious. He observed that peas grew poorly in water in which peas had previously grown, but that wheat grew readily in it. Perhaps his most striking experiment was one in which one portion of the root-system of *Mercurialis* was placed in a solution of lead acetate and the other in pure water. In a few days the pure water was found to contain the salt, and he concluded that it had been carried through the roots and excreted.

Roper (1833) called Macaire's results in question on the basis of the difficulty of freeing the roots from soil without injuring them. Unger (1836 : 147) shared this doubt, and believed that the results might also have been due to capillary action. He employed *Lemna minor* in order to avoid injury to the roots. Plants were placed in a dilute solution of sugar of lead for 8 days, washed in distilled water, and then kept in the latter for 3 days. The most sensitive tests of the latter failed to show any traces of lead, and consequently showed that no excretion had occurred. The experiment was then reversed by placing plants of *Lemna* for various periods in a salt of ammonium and subjecting them after thorough washing to a concentrated solution of lead acetate. In spite of proof that the salt had been absorbed, no trace of it could be found as an excretion into the solution.

Daubeny (1835) found that strontium nitrate absorbed by one-half of a root was not excreted by the other half, but when potassium chromate or ferrous sulphate was used, a trace seemed to be secreted into the distilled water. In a later investigation that has become classic (1845), he grew 18 different crops continuously on the same plots and compared the yields with those of crops shifted so that each crop was followed by one of a different kind. There was a gradual decrease in nearly every case, and this was usually greater with continuous cropping. However, the differences between continuous cropping and rotation were insufficient to justify the assumption of a soil toxin. They were attributed to the more rapid removal of the needed nutrients in the plots continuously cropped, and this was borne out by soil and ash analyses, leading to the distinction between available and non-available nutrients in the soil.

Braconnet (1839) also thought that Macaire's results were due to capillarity or to a siphon-like action. His attempt to obtain opium from soil in which poppies had grown was unsuccessful, as was also that of Walser (1838). Both investigators showed, moreover, that the solid excretions found by Brugmans were nothing but the exfoliated outer layers of the root.

Boussingault (1844) reached the conclusion that roots do not normally excrete substances, though they may do so in water cultures.

Garreau and Brauwers (1858 : 186) were of the opinion that the exfoliated matter left in the soil by the growth of roots served to explain the antipathy of certain plants for others.

Cauvet (1861 : 320) concluded that roots physiologically sound did not excrete poisonous or other substances absorbed by any portion of the plant. He maintained that the theories of Macaire, Chatin, and Bouchardat were not well grounded, and that the theory of rotation advanced by DeCandolle and supported by Macaire and Liebig was based upon error. He declared that the sterility of a field after cultivation was not due to the deposit in the soil of material injurious to plants of the same species. Differences in the amounts of nutrients absorbed were ascribed to the selective power of the roots rather than to the effect of root excretions.

The Woburn researches.—These have been carried on at the Woburn Experimental Fruit Farm and at Ridgmont, England, since 1897, by Bedford and Pickering. The results have been communicated in the first, second, third, fifth, and thirteenth reports, for 1897, 1900, 1903, 1905, and 1911, respectively, and in various papers. A résumé of the first four reports has been given by Livingston (1907 : 10). A summary of the investigations for the period of 16 years is given in the report for 1911, and it appears desirable to repeat it in full:

"The action of grass on fruit trees is often so deleterious that it arrests all growth, and even causes the death of the tree. In none of the experiments on the subject, which have now extended over sixteen years, has any recovery from the effect been noticed, except in cases where the roots began to extend beyond the grassed area. But trees which become grassed over gradually during the course of several years, apparently accommodate themselves to the altering conditions, and suffer much less than when the grass is actually sown over their roots. It is partially due to this circumstance that the effect of grass in commercial orchards is often less than that observed in the experimental plots at the farm; whilst another reason for differences in the results is that the effect undoubtedly varies in intensity in different soils, though the instances where the effect appears to have been nil are very rare. The fact that a tree has become well-established in the ground before the land is grassed does not, however, prevent it from suffering from the grass; trees at the farm were grassed over four years after they had been planted, and they were so much affected that many of them were nearly killed; and other trees—standards as well as dwarfs—when similarly treated twelve years after planting, are behaving in the same way, though they did not suffer so severely till the third or fourth season after grassing.

"Some varieties of apples—dependent, no doubt, on their vigour of growth—evidently suffer less from grass than others, but very little difference has been found between the effect on standards on the free stock, and dwarfs on paradise, and no explanation of the difference in the grass-effect in different soils can be traced to the depth of good soil available for root-development. The baleful effect of grass is by no means confined to apples; pears, plums, and cherries were found to be affected by it in the same way, and to, probably, nearly the same extent; though in the case of these trees the standards suffered less than the dwarfs.

"It is possible that in some soils where the effect produced is not great, grass might be advantageous from a commercial point of view, for the check given to the growth of the tree tends to increase its cropping, and grass affects the colouring matter of all parts of the tree, generally resulting in a high

colouring of the fruit. Such results were obtained at Ridgmont when the ground was grassed up to 5 or 6 feet from the stem of the tree.

"To what distance grass should be removed from a tree so as to have no effect on it, must, naturally, depend on the nature and size of the tree, as well as on the nature of the soil; with freshly planted standard apple trees, in soil which was not specially favourable to the action of the grass, a very considerable effect was produced when the grass was 4 feet away from the stems: on the other hand, keeping a space free of grass extending only 6 inches from the stems of freshly planted dwarf trees was found to have some beneficial effect, even in the Ridgmont soil. The proportion of roots extending into the grassed ground which are sufficient to make the grass-effect apparent, is remarkably small, amounting in some cases examined to only $\frac{1}{2000}$th of the weight of the whole tree.

"Forest trees appear to be affected by grass in the same way as fruit trees when the grass is sown immediately after planting; six different kinds were examined, both at Ridgmont and in some light sandy soil. The only difference in the behavior of them and of the fruit trees was, that, in the case of conifers planted in light soil, the effect was much less than with other trees, and some recovery occurred with them as time went on, instead of the effect becoming intensified.

"The action of eighteen different grasses on apple trees was examined with the general result that the action in all cases was considerable, but was greater with the strong-growing grasses than with the weaker ones. Clovers had a similar stunting effect, but the lightness in the colour of the leaves, conspicuous with trees under grass, was absent when clover was grown.

"The question of the action of grass being explicable by its affecting the aeration of the soil, by its altering the amount of carbonic acid present, or by its effect on the soil-temperature, was investigated some years ago, and any explanation on such grounds was found to be inadequate. The question of soil-moisture and of food-supply was also investigated, with a similar result, and further evidence has much strengthened these conclusions.

"As regards soil-moisture, there are general grounds for regarding a deficiency of such moisture as affording no explanation of the effect of grass on trees, for this effect is produced in wet seasons as well as in dry ones, and trees which are affected show none of the usual signs of suffering from drought; indeed, when vegetation suffers from drought, it is the grass which shows the effect much sooner than the deeper rooted trees. Determinations were made of the water contents of grassed and tilled soil at Harpenden at intervals throughout a year, and it was found that the grassed soil was slightly the wetter of the two from the beginning of January till the end of March, after which it became the dryer, but the water contents never fell below the limit which has been found to be favourable for plant-growth, although in this very soil, when grassed, the trees were showing all the symptoms of grass-injury. In the plots at Ridgmont, where dwarf apple trees have suffered so much from grass, various determinations have all shown that the grassed soil during the summer is actually wetter than the neighboring tilled ground. What the explanation of this anomalous state of things may be, is not known, but it effectually disposes of the view that the grass-effect there is due to lack of moisture. In some experiments the moisture in the soil has been increased to various extents by supplying the trees every week with water through pipes under their roots, and, though such trees were slightly benefited by this treatment, they still continued to show the effect of the grass very strongly, and were far less vigorous than similar trees in tilled soil, though this was much dryer. Still more conclusive experiments were made by growing trees i n pots, and keeping the water contents up to the same point, by watering

them two or three times a week; but even when the grass-roots were prevented from coming into contact with the tree-roots by a layer of wire gauze, and when the water was supplied from below, so that the tree got all that it wanted first, the effect of the grass on it was nearly as great as ever.

"As to the food-supply, it is difficult to see how the tree can suffer from want of nourishment so long as the soil is rich and the water-supply is sufficient. The trees in the grassed plots have been manured annually just like those in the tilled plots, and the grass crop is not removed, but is left to rot on the ground: the soil of these grassed plots may be poorer by the amount of material in the one crop which is actually growing on them, but in a series of years this would represent a removal of food-material far smaller than that removed by the vigorously growing and cropping trees in the tilled plots: indeed, it is well known that grass crops, if properly manured, actually enrich the soil, and it has been found by direct experiment that, when trees are grown in soil taken from the grassed plots, they flourish better than in soil taken from the tilled plots. Various other experiments have been made on the subject, of which it is only necessary to allude to some pot experiments, similar to those mentioned above, in which nourishment was supplied with the water, without effecting any appreciable reduction in the action of the grass, though the soil was thereby rendered richer than it was in the pots without grass, where the trees were growing vigorously. It is evident, therefore, that the grass-effect cannot be explained by any lack of nourishment: if the immediate cause is starvation, it is starvation in a land of plenty, due to some other factor which prevents the roots from availing themselves of the food which is there.

"Amongst the possible causes of the action of grass, that of a physical alteration in the soil has been examined, but with negative results. The grass might either by mechanical or chemical means cause an accumulation of very fine soil particles at a depth corresponding with that of the tree-roots, and so interfere with the functioning of these. But mechanical analyses of several grassed and tilled plots of ground failed to reveal any alteration in the distribution of small soil particles which would account for the effect of grass. Other experiments in which the soil was made alkaline, showed that the grass-effect could not be attributed to alkalinity produced by the grass in its growth.

"Incidentally, the physical alteration produced in soil by rendering it alkaline with potassium carbonate was investigated and found to be surprisingly small.

"The question of soil bacteria was also partially examined. The numbers of such bacteria in some grassed soil in which trees had been suffering from the grass-effect was found to be considerably greater than in the neighboring tilled soil; but this could not account for the grass-effect, for such an effect was equally apparent in the case of trees grown in sand, where the number of bacteria present was found to be much less than in tilled soil.

"In connection with this question trees have been grown in soil which had been partially sterilized by heating to different temperatures, and they have been found to behave in the same way as other plants. The action of heat on a soil results in the destruction of the greater part of the bacteria present in it and the total destruction of certain protozoa, which feed on the bacteria; the result of which is that, after a certain lapse of time, the bacteria left in the soil multiply without check, and the soil becomes richer in bacteria, and in the nitrates formed by them, than it was originally; such soil is specially favourable to plant-growth; at the same time, however, the heating results in the production of some substance which is actively toxic toward plant-growth, and so long as this is present, plants will not flourish in it. But the

toxin is rapidly oxidized by the action of air and moisture, and is destroyed under cultivation in a few weeks. In soil which has been heated, therefore, plants will not thrive at once, especially if the supply of air is restricted, though after a time they grow better in it than in soil which has not been heated at all. Thus plants may behave in diametrically opposite ways in heated soil, according to the conditions under which they are grown. This has been found to be the case with apple trees, as well as with grasses and other plants.

"The toxic substance produced by heating soils was found to be toxic toward the germination of seeds as well as toward the growth of plants, retarding the germination and reducing the percentage of seeds which germinate. In extreme cases seeds may take five or six times as long to germinate in heated as in unheated soil. As experiments on seed-germination can be carried out in a day or two, whereas those on plant-growth require many weeks, during which the character of the soil may become materially altered, the former offered a promising means for searching for the presence of toxic matter in grassed soil. A considerable number of instances were taken in which grassed and tilled soils within a few feet of each other were examined as to their behaviour toward germinating seeds, and the examination was conducted at three different seasons in the year; but the results in every case showed, contrary to expectation, that the soil from the grassed ground was slightly more favourable toward germination than the tilled soil. These results, of course, afford no direct evidence in favour of the presence of a toxic substance in grassed soils, though they are quite consistent with such a view, for a toxic substance, if present, might, just as in the case of heated soil, give rise, on decomposition, to conditions specially favourable toward germination. It was noticed also that in most cases the soil which had been under grass absorbed water much less readily than the neighbouring tilled soil, a behaviour which is highly suggestive, inasmuch as the same character is observed in heated soils, in contrast with unheated ones.

"Strong evidence of a positive character as to the formation of a toxic substance during the growth of grass was finally obtained from various series of experiments with trees grown in pots. It was found that such trees, when watered with the leachings obtained from trays containing grasss growing in sand, flourished more than when water alone was supplied; but when the trays were placed on the surface of the soil (or sand) in which the trees were growing, so that the washings from the grass reached the tree-roots with practically no exposure to the air, they then had a very deleterious effect, nearly, if not quite, as great as when the grass was grown above the roots of the trees in the ordinary way. The trays containing the grass were movable, and the sand in them, with the grass growing in it, was separated from the medium in which the trees were growing by the perforated iron bottoms of the trays and a sheet of wire gauze; moreover, the contact between the bottoms of the trays and the sand or soil beneath would be, at the best, very imperfect, so that it is impossible to explain the action of grass in such a case by the abstraction by the grass of anything from the soil (or sand) below the trays, and it must be due to the passage of something from the trays down to the trees. The experiments on this subject were numerous, and the grass-effect was uniformly shown in all of them; and, it should be mentioned, the trees without grass, with which the grassed trees were compared, were grown with trays of sand above their roots, so as to exclude the possibility of explaining the results by the mere presence of the trays.

"The ready oxidisability of the toxic matter formed by grass into some substance which favours plant-growth will explain the previously observed beneficial effect of grass-leachings in cases where these had been exposed

to air, and also why soil taken from grass-grown ground should be more favourable to plant-growth than that from tilled ground. All this is in full accordance with what has been established as to the behaviour of heated soils towards plants, where toxic matter is formed by the heating, and increased fertility follows its destruction, and is in accordance, also, with the results obtained with the germination of seeds in soil from grassed and ungrassed ground, the time elapsing between the drawing of the samples and the germination of the seeds being sufficient for the conversion of any toxic substance present into a beneficial substance."

Bedford and Pickering (1914) stated that every growing crop results in the formation of a substance toxic to the growth of other plants, and still more so to itself. By oxidation this toxin loses its properties and increases the fertility of the soil. There is no reason for assuming that the toxin is excreted by the plant. The root débris from the growing roots is probably sufficient to account for its formation, or an alteration in the bacterial contents of the soil due to the growth of the grass. In heated soils a toxin is formed by the action of heat alone, and the subsequent oxidation of the toxin can occur without the agency of bacteria. There is no reason to suppose that changes in the organic débris of a growing crop may not equally occur without the action of bacteria, though in all probability they may be materially aided by them.

Pickering (1917 : 181) has carried out experiments for the purpose of securing direct proof of the production of toxic substances by growing plants. Three flower-pots with mustard plants were fitted with trays containing 5 inches of soil and with an aperture for the plants. One tray contained a crop of mustard and had a perforated bottom, so that water could pass through to the pot; a second had the perforations closed, so that no water could reach the plants below; and the third contained soil, but no plants. The mustard plants below the last two trays grew normally, but those below the first were reduced to a hundredth of the normal growth. It was regarded as obvious that the leachings from the plants in the trays contained a substance toxic to other plant-growth. By means of this method, apples, cherries, plums, pears, 6 species of forest trees, mustard, tobacco, tomatoes, barley, clover, and 2 kinds of grasses, were found to be susceptible to toxins, and apple seedlings, mustard, tobacco, tomatoes, 2 kinds of clover, and 16 of grasses were found to produce toxic effects. In pot experiments the effect varied from a reduction in growth of 6 to 97 per cent, while in field experiments with trees the effect ranged from slight to fatal. The possible factors eliminated were protection and moisture, variations of temperature, alkalinity and physical condition of the soil, carbon dioxid, and bacteria, but it is disappointing not to have the details of these experiments. As to the source of the toxin, it is said that while excretion from the roots is possible, the dejecta left by the roots in the soil may account for the toxic properties just as well as exudates.

Researches of the Bureau of Soils.—The most extensive series of investigations have been carried on by the Bureau of Soils of the United States Department of Agriculture from 1905 to 1915. The pioneer study of this series was by Livingston, Britton and Reid (1905), who grew wheat seedlings in untreated Takoma soil and its aqueous extract, as well as in these when modified by various substances. Native and cultivated plants growing on Takoma soil exhibited structures similar to those of a soil subject to drought, and wheat seedlings were much stunted, even though the water-content was kept constant. When grown in aqueous extracts of the soil they made the same kind of growth as in the soil itself. The dwarfing effect of both soil and extract was reduced by the use of stable manure, pyrogallol, calcium carbonate, etc. It was regarded as very well established that Takoma soil contains some substance or substances toxic to wheat plants, and as also indicated that bodies are given off by the roots of growing wheat plants deleterious to them or to other wheat plants following them. It is suggested that the so-called exhausted soils are really poisoned and that crop rotation is beneficial because it prevents the accumulation in the soil of the injurious excreta of any one form of plant life. In further studies, Livingston (1907) stated that injurious substances similar to those existing in soils are produced by the growth of wheat in water or sand cultures.

Schreiner and Reed (1907) maintained that the unfavorable conditions brought about by root excreta may affect the succeeding crop if immediately planted. When wheat succeeds wheat the effect is very marked, and it is also marked when wheat follows oats, but there is little or no effect when it follows cowpeas or corn. They tested the effect of more than 30 different organic soil constituents on wheat seedlings, and found that the majority of them caused injury in concentrations ranging from 1 to 50 parts per million. The toxic solutions were markedly improved by treatments similar to those that benefit the extracts of unproductive soils. When succeeding crops were grown in the same soil, certain fertilizers were found to act very beneficially upon soils containing the toxic excreta of plant roots. Methods of cultivation that promote the aeration of the soil and the growth of micro-organisms may aid in destroying soil toxins, and their undue accumulation may be prevented by proper crop rotation.

Schreiner and Reed (1907[2]) have discussed the rôle of the toxic excreta of roots, and suggested that they may be of importance in plant succession, as well as in determining the composition of plant communities, such as the characteristic "oak openings." The excreta of growing roots are also regarded as one of the main causes of the low yields obtained in improper crop rotations. While the production of toxic excretions by the roots of plants is undoubtedly a factor of importance in soil fertility, they probably do not accumulate to a harmful extent in soils kept in good tilth. Proper aeration

will do much to destroy them, by favoring the decay of organic matter through the activities of soil organisms and the processes of oxidation.

Jensen (1907 : 872) has tried the effect of tree seedlings on the growth of wheat in paraffined wire pots, in which the water-content was maintained by frequent watering. The results showed a decrease in the green weight of the wheat grown in the pots with the tree seedlings. It is pointed out that this can not be due to shade, to water-content, or to the nutrient content, and it is assumed that the retarding effect is due to substances excreted by the tree roots. The conclusion is reached that tree seedlings of the tulip-tree, dogwood, maple, cherry, and pine retard the growth of wheat, when the roots of the latter are in close physical relation with the tree roots. The retardation differs with the species and is greatest while the tree seedlings are most active physiologically. The final conclusion is to the effect that the injurious action of trees upon wheat appears to be due to the excretion of substances by the tree roots, which are toxic to the growth of wheat.

Schreiner and Shorey (1909) isolated four organic compounds from soil, of which two, picoline carboxylic acid and dihydroxystearic acid, were found to be harmful to wheat seedlings, the second in all concentrations, and the first in that of 100 parts per million. The results were stated to furnish simple tangible proof that injurious organic compounds exist in unproductive soils and to lay the foundation for the rational study and improvement of unfavorable conditions. In further studies of dihydroxystearic acid, Shreiner and Skinner (1910) have found that it retards the growth of wheat plants when present in solution in pure distilled water at the rate of 50 parts per million. It was likewise harmful in the presence of nutrient and fertilizer salts in all ratios of $P_2O_3NH_3$, and K_2O, but least harmful in the ratios best suited to plant growth. The direct effect of the acid is to darken the root-tips, stunt root development, and inhibit strongly the oxidizing power of roots. The fertilizer combinations that tend to increase root oxidation are also those that minimize the harmful effects. Schreiner and Lathrop (1911) have examined 60 soils from 18 States, and have found dihydroxystearic acid in half of the 35 soils classed as poor and in but 2 of the 25 good soils. This acid is regarded as a direct factor in the low productivity of soils by virtue of its harmful effect on growing crops, or as an indirect factor, serving to indicate other harmful compounds or conditions.

Schreiner and Skinner (1912) have isolated a number of nitrogenous constituents from the soil, and tested their effect upon wheat seedlings. The majority of these, such as nucleic acid, xanthine, guanine, creatine, choline, etc., exert a beneficial effect and are able to replace nitrate in its effect, while others, such as picoline carboxylic acid and guanidine are harmful. It is thus clear that the soil contains both beneficial and harmful compounds, and the predominance

of the one or the other depends upon soil conditions, composition, drainage, plants, etc., all of which are affected by tilling, cultivation, draining, liming, fertilizing, and rotation.

Shorey (1913) has carried further the study of organic soil constituents, and has isolated the following compounds from widely separated soils: oxalic, succinic, saccharic, and acrylic acids, lysine, adenine, choline, trimethylamine, salicylic aldehyde, mannite, rhamnose, trithiobenzaldehyde, nucleic acid, and an unidentified aldehyde. This brings the number of compounds isolated to 35, of which 13 are organic acids, 9 organic bases, 3 sugars, 2 aldehydes, and 2 alcohols.

Schreiner and Reed (1909) have confirmed the results of Molisch (1888), Czapek (1896), and Raciborski (1905) as to the oxidizing power of the roots of growing plants, finding this to be greatest in the root-hair region. The oxidizing power is greater when plants are grown in an extract of productive soil than in one of an unproductive soil. Oxidation was usually favored by adding an absorbing agent to the extract, as well as by the addition of nitrates, phosphates, and calcium salts. Toxic organic substances in solution were extremely injurious to the oxidizing power, which was able to reduce the toxicity, however, especially in the presence of nitrates. Oxidation by roots is due largely if not entirely to the acitivity of a peroxidase produced by them. This enzyme is most active in neutral or slightly alkaline solutions, and its action may be inhibited by acids as well as by putrefaction processes. Oxidation by roots is of agricultural interest, since the promotion of oxidation is an important factor in tillage and cultivation.

Schreiner and Sullivan (1910) have studied oxidation in the soil and conclude that it plays an important part in the organic and inorganic changes that occur. It appears not to be enzymotic, but the result of interaction between inorganic constituents and certain kinds of organic matter. It may also be brought about by organic matter in a state of autoxidation and by inorganic oxygen-carriers, such as manganese and iron. Oxidation was increased by the addition of salts of manganese, iron, aluminum, calcium, and magnesium. Some kinds of organic matter, such as dihydroxystearic acid, inhibit soil oxidation, but in general a plentiful supply of organic material promotes oxidation. Excessive oxidation, however, is harmful to vegetation. The oxidative power of the soil is regarded as a sympton of its condition, so that whatever decreases oxidation tends also to bring about the conditions that decrease growth, while the factors that favor oxidation are those that promote productivity.

Sullivan and Reid (1912) have shown that soils possess the power to decompose hydrogen peroxid, and that this is greater in soil than in subsoil and in strong than in weak soils. In general, the catalytic power of soils seems to be due not to an enzyme, such as catalase, but rather to the separate or joint activity of the inorganic and

organic matter. Strong catalytic power in a soil may be taken as evidence that the many factors of soil fertility will be prominent and the soil will be productive.

Skinner (1913 : 342) concluded that soil which had grown sesame contained substances that were harmful to cabbage plants, but not to wheat seedlings. Field observations showed that the soil in which sesame had grown was injurious to cabbage, while in the same soil without sesame, cabbage grew well. It is assumed that plants are affected by the remains of previous vegetation or plant growth, and that the effects are more or less specific, injuring one species and not another. Since the plants grew much better in soil solutions shaken up with carbon black, it seems possible that a lack of oxygen or an abundance of CO_2 was responsible.

Other researches.—Jones and Morse (1903) have observed an apparent antagonism between the butternut and *Potentilla fruticosa*, and attribute this to the root relations rather than to the shade. The invasion of the soil by the vigorous roots of the butternut near the surface is thought to interfere with the nutrition of the cinquefoil in some manner. It seems probable that this is a combined light and water relation, since "it is stated that the shrubby cinquefoil is quickly killed by tree-growth of any kind," especially since it is more or less hydrophytic. "If the stock is fenced out of a field the trees will soon come in and the cinquefoil weaken and die out as the trees overshadow it."

Hedrick (1905) observed that young peach trees shed their leaves and matured quickly when oats were planted in pots with them. Potatoes or tomatoes wrought less injury to the trees, mustard and rape had but slight effect, and beans and crimson clover none at all. The leaves turned yellow before falling, indicating drought resulting from the competition. The effect of a grass sod upon apple trees was later investigated (1910). The grass was cut once or twice each year during the 5 years, while the tilled plot was plowed each spring, cultivated 4 to 7 times until late July, and then planted to a cover-crop. The average yield on the sod plot for 5 years was 72.9 barrels and on the tilled plot 109.2 barrels per acre, while the average weight per apple was 5 and 7 ounces, respectively. The average gain in trunk diameter was 1.1 inches in sod and 2.1 inches under tillage, and the average leaf weight was 9.7 gm. and 11.5 gm., respectively. The average annual growth of branches for sodded trees was 1.9 inches and 4.4 inches for tilled trees, while the average number of laterals per branch was 3.4 for one and 6.7 for the other. These differences are ascribed to water-content, the latter being highest in the tilled plot. Aeration and bacterial activity are regarded as playing some part in the results.

The effects of various methods of culture upon the growth and production of the apple have been investigated by Green and Ballou (1906). An orchard was divided into four plots, each of which was given different treatment. In the cover-crop plot, the ground was plowed or disked early in the spring, cultivated until late in July, and then sown to a cover-crop. The plot with clean culture was treated similarly, except that cultivation continued through the growing-season and no cover-crop was employed. The sod-culture method consisted in planting the trees directly in sod and in cultivating a circle of 3 or 4 feet around the tree throughout the season. The grass was cut several times each season and allowed to lie. In the sod-mulch plots, the treatment was the same, except that the circular area was mulched with straw and the cut grass used to maintain the mulch. Continuous clean culture was abandoned after four seasons, owing to the washing of the soil and the removal of the vegetable matter. The trees made the heaviest and most uniform growth in the sod-mulch plot, in comparison with good growth in the cover-crop plot, and much poorer in the sod-culture one. The average diameter of the trees in the three plots was 10.56, 9.71, and 8.55 inches, respectively. The greater growth under sod-mulch was ascribed to the greater supply of food-material under the mulch.

Dandeno (1909 : 24) assumed from field observations that grain grew better when associated with Canada thistle, and tested this experimentally by planting oats, barley, wheat, buckwheat, and flax separately in pots, as well as with a vigorous underground shoot of Canada thistle in a second series of pots. In another series young elm trees were planted singly in 6-inch pots, and oats grown with them. With the exception of buckwheat, all the plants grew as well or better with the Canada thistle as alone, the stimulating effect being most pronounced at 22 days after planting. On the contrary, the elm tree had an injurious effect, as all species grew more poorly with it. It was suggested that the results were due on the one hand to the excretion of substances that stimulate growth or release plant food, and on the other to the excretion of harmful substances.

Howard (1910, 1915) has found that grass has a marked effect upon most species of fruit trees at Pusa. The leaves are few, very small, and pale yellow; the leaves and flowers appear much later than normally, and the leaves fall early. Very little new wood is formed and the growth in height is much less. The fruit from trees under grass is smaller, less abundant, as well as less juicy and of poorer flavor. The effect of grass is greater with small trees than with large ones, and *Cynodon dactylon* is more injurious than *Imperata arundinacea*. This difference in the two grasses seems to be explained by the fact that *Cynodon* requires more air, and correspondingly reduces the supply to the tree roots. Moreover, the Pusa soil packs to such

an extent that the accumulation of carbon dioxid is favored, and it is suggested that this may be the toxin concerned.

Russell (1912 : 111) grew six crops of rye in succession in sand to which only nutrient salts were added to keep the food material constant. A seventh crop was then grown at the same time as one on perfectly fresh sand on which no crop had ever grown, though it was also supplied with an equal amount of the same nutrients. Similar experiments were made with buckwheat and spinach, and a parallel series was carried out in soil cultures. There was no significant difference in the two crop yields, except in the case of buckwheat in sand, an exceptional result that could not be confirmed. If the rye, buckwheat, or spinach excreted any toxin, the amount accumulated during the growth of the six successive crops was insufficient to depress the yield of the next crop appreciably. Thus, no lasting toxic effect at least was produced by any of these crops, and the toxin hypothesis fails to explain the advantages of rotation where there is always a lengthy interval between crops. It is concluded that there is no evidence of soluble toxins in normally aerated soils sufficiently supplied with plant-food and with calcium carbonate, but toxins may occur on sour soils badly aerated and lacking in calcium carbonate, or in other exhausted soil. There is no evidence of any plant excretions conferring toxic properties on the soil, but the Woburn results show that a growing plant may affect its neighbor.

Sherff (1912 : 428) observed that *Sagittaria* was able to invade ponds of *Nymphæa* from the reed-swamp only when *Nymphæa* was nearly or quite absent. The rhizomes of the latter are usually decayed well toward the growing apex, and generally when the rhizomes of *Sagittaria* penetrate the decayed parts, they also begin to decay. Where the decayed *Nymphæa* rhizomes lay nearer the surface, *Sagittaria* had grown underneath without harm.

Hall, Brenchley and Underwood (1913, 1914) have studied the growth of plants in soil solutions with especial reference to the theory of Whitney and Cameron, and have obtained the following results:

"We may now consider how far these results bear on the theory that crops leave behind in the soil specific toxins which depress the growth of succeeding crops of the same kind. In Series I, wheat and barley yielded almost exactly the same weight of plant, whether they grow in solutions from the wheat or the barley soils. As a rule the wheat plants were a little heavier when grown in the solutions from the barley soils than when grown in solutions from the corresponding wheat soils, but the barley plants were similarly heavier in the solutions from the barley soils. The ratio of root to shoot is very close in the two sets. Again, wheat and barley grown in the same solution yield weights agreeing within the range of error of such experiments. These facts alone would dismiss the hypothesis that the wheat soils contain any soluble toxin injurious to wheat but not to barley, and *vice versa*, notwithstanding the 60 years' repeated growth of these crops on the same soils. In Series II the demonstration was pushed a stage further by including in the comparison an artificial culture solution made from pure salts and con-

taining phosphoric acid and potash in the same proportions as the solutions from the completely manured plots. Another set of the soil solutions was boiled before use, since boiling had been reputed to destroy the toxin and would at any rate kill off any bacteria that might be factors in the result. Lastly in another set the solutions were evaporated, the residue ignited and dissolved afresh in a minimum quantity of hydrochloric acid, then diluted to the original volume.

"In this series boiling was without effect, whether the solutions contained added nutrients or not; the residue left on evaporation, after ignition and re-solution, gave generally lower results, in some cases to a marked degree. The soil solutions from completely manured plots gave higher yields than the artificial solutions of corresponding strength. In order to ascertain whether the results were limited in any way by the nature of the plant (it might be objected as regards Series I that barley and wheat are so closely akin as to excrete the same toxin) the experiments in Series II were repeated with sunflowers, white lupins, and buckwheat.

"These plants are far from being so suitable for experiment as barley, and the results are somewhat erratic (e. g., white lupins gave almost their maximum yield in the solution from the unmanured plot, indicating that growth had been mainly sustained on the original food-store in the seed), but they in no way indicate the presence of a toxin in the soil solutions which depresses the growth of barley, but *ex hypothesi* is without effect on plants of another order. Finally in Series III, both barley and peas grew as freely in the soil solutions from the completely manured plots and in the solutions from the incompletely manured plots after repair of the deficiency by adding salts, as in the artificial solutions made up with pure salts. Indeed the superiority, though hardly large enough to be significant, lay with the plants grown in the soil solutions. Thus the experiment yielded no evidence of the existence in soils on which a particular plant had been growing for 60 years and upwards, of a soluble 'toxin' having a depressing effect upon the growth of that plant."

Lyon and Bizzell (1913 : 38) have conducted a series of experiments on the stimulating influence of plants on each other. These were made by planting primary plants or crops, followed by secondary ones at a somewhat later time. In the case of greenhouse soil and of nutrient solutions in crushed quartz, the yield of the primary crop in mixtures was greater than when it was grown alone, in just the same number of cases as it was less. When the primary crops and mixtures were grown on field soil, the yield of the primary crop and the mixture was greater in 11 cases and less in 4. Moreover, it was found that the so-called stimulus is stronger during the early part than during the later part of the life of the plant. This is indicated by the field experiment, in which nearly all of the primary crop harvested at bloom gave a larger yield in combination than alone, while similar mixtures allowed to mature, gave opposite results.

Bottomley (1914 : 531) has found that "bacterized" peat acts as a stimulant to growth, and that phosphototungstic and silver fractions derived from it show the effect of the accessory food factors of Hopkins and to some extent of the vitamines of Funk. He concludes that the nutrition of a plant may depend upon the presence of these

accessory food substances, as well as upon mineral nutrients, and thinks that the very small amounts necessary are at first supplied by the seed and later by the humus of the soil. Bacterized peat results from the action of certain aerobic soil organisms at 26° C. which decompose it and convert a large amount of the humic acid present to soluble ammonium humate.

Bergen (1915 : 491) observed that an exceptional rainfall in July led to much greater growth in perennial mesophytes growing alongside of a belt of deciduous trees. The stems of *Aster novæ-angliæ, Asclepias tuberosa,* and *Helianthus grosse-serratus* were about twice as tall and much more robust than during the ordinary season. A suppressed plant of *Chelone glabra* grew luxuriantly and flowered freely. The dwarfing in ordinary seasons was ascribed to the lower water-content, due to the demands made by the trees.

Amos (1918), in a study of the causes of clover sickness, finds scant evidence that it is due to the excretion of toxic substances by the preceding clover crop.

Hartwell, Pember and Merkle (1919) have conducted experiments on the effect of one crop upon another, in which five different crop plants were grown for 2 to 3 years in the same soil, and then followed by a particular crop plant. When onions were grown after each of the individual crops, the yield was least with buckwheat and mangels, larger with rye and onions, and best with redtop. When buckwheat was the succeeding crop its yield increased after crops in about the following order: redtop, buckwheat, mangels, rye, and onions. The divergent effect of crops on those that follow seems not to be due, principally at least, to the amount of nutrients removed, since the smallest yield may not occur after the crop removing the largest amount of the nutrient most needed. Soil acidity was affected differently by the various crops, and generally the best yield of onions, which are sensitive to the conditions accompanying acidity, followed the crops giving rise to the least acidity. This relation was supported by the fact that the effects of the crops on the following one were much less divergent when acidity was reduced by liming.

CONCLUSIONS.

The original assumption of Livingston, Schreiner, and their associates, and of Bedford and Pickering as well, to the effect that plant roots excrete substances toxic to the plants themselves and to other plants, seems no longer to be accepted even by them. While Livingston (1918 : 93) regards the general hypothesis that unproductiveness in agricultural soils is frequently due to soil toxins as well established and generally accepted, he states that:

"The evidence that crop plants do actually excrete toxic substances into the soil is not very strong in any of this work. Better than to assert that they are so excreted is to state that there is evidence that the soil frequently

contains toxins, and that these sometimes result, directly or indirectly, from the growth of higher plants. As to the manner in which these poison substances arise in the soil, no definite statement can yet be made, but they are surely not generally excreted *as such* from the plant roots. That such poisons *are present* in many soils has now been extablished without question by Schreiner and his coworkers, and also that their deleterious effects may often be removed by oxidation, or by the addition of proper substances."

Pickering (1917) says: "But though their excretion from the roots is possible, there is no need for imagining such an occurrence; all plants in growing leave much root-detritus in the soil, and such dejecta may account for toxic properties just as well as ejecta."

However, if he is right in ruling out deficient aeration and carbon dioxid as causes, then both of these statements appear incorrect, since it has been shown over and over again that under normal conditions roots excrete no other toxic substances than carbon dioxid, and the aerobic fermentation of plant material rarely produces toxins. There seems to be no doubt that roots do not excrete other toxins than carbon dioxid, except under anaerobic conditions, and the results drawn from cultures in solutions are either to be explained by deficient aeration or by the limitations of the method itself, as indicated by Stiles (1915), Hoagland (1919), Jordan (1920), and Davis (1921).

The statement of Bedford and Pickering (1914) that every growing crop results in the formation of a substance toxic to the growth of other plants, and still more so to itself, would seem to require that the fruit trees of an orchard or the trees of a grove or forest should be more toxic to each other than to grass or grass to them. However this may be, the results of other investigators warrant Howard's suggestion (1915 : 23) that carbon dioxid should not be finally dismissed as the toxin concerned, without repeating the Woburn experiments dealing with this gas. He finds that the results obtained by Bedford and Pickering with tobacco are exceedingly like those observed at Pusa when tobacco is water-logged or grown on heavy lands that have been green manured. Since tobacco requires a great deal of air and green manuring produces much carbon dioxid in the soil, it seems probable that the Woburn results, in which grass washings injured tobacco, may be due after all to the inhibiting effect of carbon dioxid. This may be the toxin about which so much is written, and it may prove to be the cause of the effect of grass on trees, as well as of one crop on another. In many parts of England grass is grown under fruit trees without particular damage, but in most of these the soil is very porous, and the carbon dioxid diffuses without doing harm. The soils at Woburn and Pusa are not porous, and in such dense soils the effect of carbon dioxid should be far greater than in the porous soils of Kent.

Hole (1918 : 439) has also pointed out the probable significance of defective aeration for the problem at Woburn. A dense growth of

grass is correlated with an accumulation of dead roots, leaves, and other débris in the surface soil, which promotes the activity of soil organisms. Rain-water percolating through such a layer of grass would tend to lose its oxygen and to become heavily charged with CO_2. Pickering notes that when such "toxic matter is exposed to the air for 24 hours its toxic property is found to have entirely disappeared." Exposure to the air would tend to make good a deficiency of oxygen and to dissipate an accumulation of CO_2 by diffusion. Such an accumulation of carbon dioxid about plant roots has been demonstrated by Leather for a number of plants.

King (1908 : 626) criticized at some length the assumption that crops excrete and leave in the soil toxins which are the chief cause of reduced yields and worn-out lands, and that rotation, manuring, and fertilizing owe their good effects to destroying or removing the toxins rather than to their ability to supply nutrients. The amount of nutrients carried by the soil was discussed, and the conclusion reached that it is impossible that a mere rotation of crops, coupled with good tillage and adequate water-content, should indefinitely maintain high yields, when the whole crop above ground is regularly and continually removed from the field. Figures were given to show the extreme variation of the soil solution, and these indicated that there is no good foundation for the contention that all soil solutions have essentially the same composition and concentration, viewed from the standpoint of their function in plant-growth. Evidence was also given to show that there was a regular and corresponding increase in the yield with each increase in the amount of nitrogen, phosphorus, and potassium recoverable from the soil, and Rothamsted results were cited to prove that the soluble salt-content of soils is not constantly maintained at a point sufficient to give good crop yields. Experiments in which the toxic effect of organic compounds was determined on the basis of transpiration or green weights were regarded as misleading and indecisive, and particular objection was raised to the short term, the small amount of solution, and the generally abnormal conditions of experimentation. In short, it is concluded that nothing yet published by the Bureau of Soils or by others should in any sense be regarded as proof that toxic excreta play an important rôle in rendering soils unproductive.

Hall, Brenchley, and Underwood (1913) have tested the contentions of Whitney and Cameron, and reach the following conclusions with respect to the soil solution and the growth of plants in it:

"The composition of the natural soil solution is not constant as regards phosphoric acid and potash, but varies significantly in accord with the composition of the soil and its past manurial history. Within wide limits the rate of growth of a plant varies with the concentration of the nutritive solution, irrespective of the total amount of plant food available. When other conditions, such as the supply of nitrogen, water, and air, are equal, the growth

of the crop will be determined by the concentration of the soil solution in phosphoric acid and potash, which in its turn is determined by the amount of these substances in the soil, their state of combination, and the fertilizer applied. The net result of these investigations is to restore the earlier theory of the direct nutrition of the plant by fertilizers."

In conformity with the view that roots do not excrete toxic substances, it must be recognized that the value of crop rotation does not depend upon getting rid of the toxic exudates of a particular crop. Where such toxins as dihydroxystearic acid are present as the result of the partial decomposition of organic matter, the effect would be produced by all crops that leave residues in the soil. As a consequence, fallowing, tillage, or fertilizing, alone or in combination, would suffice to get rid of the toxin, regardless of the crop sequence. The fact that the absence of rotation for 60 years does not result in the appearance of specific toxins in normal cultivated soil has been proved by Hall and his associates (1913, 1919), in connection with the growth of continuous crops of wheat and barley on the Rothamsted plots.

Russell has also shown that the growth of 6 successive crops was insufficient to cause appreciable reduction in the yield of the next crop, and concludes that this rules out toxins as an explanation of the advantages of rotation, when there is a lengthy interval between crops. As King and Hall maintain, rotation still appears to rest upon the different nutrient and tillage relations of the successive crops, though in many soils the relation of the various crops to acidity may be an important factor, as indicated by Hartwell and his associates.

The early assumption that root secretions were a factor in plant communities and in succession is no longer valid, but apparently this is still thought of as a possibility in connection with soil toxins. In all successions, except for the early stages of the hydrosere, the amount of organic matter in the soil steadily increases, but the absence of any toxic effect is demonstrated by the fact that the number of individuals and often the number of species also increases to the subclimax or climax stage. Since a plant community regularly returns its material to the soil, the question of nutrients enters only in cases of intense competition, though their increasing availability is a factor in succession. Field studies of germination and growth and of community development, as well as competition cultures under control, have shown that water-content, air-content, nutrient-content, and temperature are normally the primary factors, more or less modified by competition. Innumerable seedlings have been found to grow as well in parent communities as in those of other species, and consocies of annuals have been known to maintain themselves for 10 to 20 years, and to yield only when invasion became overwhelming.

Many successional stages and climaxes have been under detailed observation in Nebraska and Colorado since 1896, without the slightest evidence that toxins are in any manner concerned in their condition. Some of these are more luxuriant than when first seen, and a close study of their growth from year to year has shown that it varies only in relation to the rainfall and the resulting water-relations. It seems certain that most climaxes have occupied their habitats for thousands of years, or even longer, and that their present growth and composition make the depressing effect of toxins unthinkable. In short, they extend the Rothamsted results with soils continuously cropped from 60 years to thousands of years.

Soil toxins are probably to be definitely related to deficient aeration and to anaerobic conditions, as has been indicated by Schreiner, Hall, Russell, and others. This is also shown by the fact that they are readily oxidized, and soon disappear under proper tillage. Hence, they appear to be due to essentially the same conditions and processes as obtain in bogs, the relationship being especially well exhibited by muck soils. In both, the primary causes of toxicity are the direct lack of oxygen and its indirect effect in permitting the accumulation of carbon dioxid in harmful amounts and in producing injurious organic acids and other compounds. In many cases probably the first two alone are concerned, but in sour soils and muck soils at least, all of them must have a part, though the lack of oxygen plays the primary rôle. Since carbonic and other acids are the products of respiration under such conditions, a considerable part of soil acidity may be ascribed to them, though it must be recognized that toxic effects may arise from acidity otherwise produced, as shown in the preceding section. In conclusion, the present facts appear to warrant the statement that organic toxins are excreted by roots or produced in soils only as a consequence of the anaerobic respiration of plant roots and of micro-organisms, and that inorganic toxins may arise as a result of chemical processes or of adsorption.

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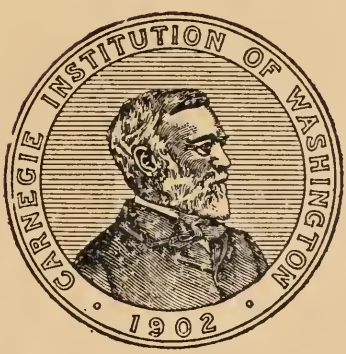
AERATION AND AIR-CONTENT

THE RÔLE OF OXYGEN IN ROOT ACTIVITY

BY

FREDERIC E. CLEMENTS



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